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THE ECOLOGY OF *PASSALUS CORNUTUS* FABRICIUS, A BEETLE WHICH LIVES IN ROTTING LOGS

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THE ECOLOGY OF *PASSALUS CORNUTUS* FABRICIUS, A BEETLE WHICH LIVES IN ROTTING LOGS

INTRODUCTION

The beetles in the family Passalidae are of particular interest because they furnish examples of primitive societies. According to Wheeler (1928) there are social insects in six families of beetles. All these live in cavities in plant tissues. Wheeler characterizes a society as an "accumulative collectivity." Among such insects as termites there are extensive architectural accumulations and a complex system of castes. These have been made possible by social life. Termites "early resorted to a food-supply which was abundant and readily obtainable but not easily assimilable." Perhaps all social life among insects was at first associated with and made possible by such dependable sources of food as wood, and later evolved more elaborate social appurtenances in the way of polymorphism, trophyllaxis, mycetophagy, etc. Today termites are well organized in a ligneous environment, but beetles are just becoming established.

Passalid beetles are common throughout the warmer parts of both hemispheres. They were first studied extensively in Brazil by Ohaus (1899). A pair make rough galleries in damp rotten logs and live there with their progeny. The eggs are laid in a loose cluster and watched over by the parents. The adults and larvae both stridulate. The former produce squeaking sounds by rubbing the abdomen on the wings; the latter have a reduced pair of hind legs which they rub against the sides of the body. Stridulation serves to keep members of a colony together. Passalids show no castes; in fact, it is difficult or impossible to distinguish the sexes by external features.

It has been believed that the larvae of passalids require food which has been triturated and mixed with secretions produced by the parents. Like all social beetles, passalids depend on an abundant vegetable food and the parents care for the young to some extent. They avoid competition with other animals by utilizing foods which are indigestible for most other types. In rotting logs they also have the advantages of protection from enemies and a certain degree of thermal and hydric stability. Wood retains water, which has a high specific heat, and thus not only furnishes necessary moisture but prevents rapid temperature changes. Organic decay tends to keep a log warm when there are extremely low temperatures outside. Park (1935) has carried out extensive experiments to test the periods of rest and activity of *Passalus cornutus*. He kept the beetles in logs and subjected them to various external conditions of light and temperature. They were active as much during day as during night. In their relatively constant environment there was little or no diurnal periodicity.

The Duke Forest furnishes abundant material for the study of the activities of *Passalus cornutus*. Many rotting logs contain extensive galleries which are occupied by colonies. Oak and hickory logs are most often used as homes, but at times gum, dogwood, sourwood, and other woods are excavated. Rarely a pair may be found in a pine log. As many as ninety-odd passali were found in one large log. These were members of several colonies.

FIG. 1. *Passalus cornutus* Fabricius: dorsal view; X 3.6.

Beetles were studied during the years 1933, 1934, and 1935. In 1933 and 1934 routine monthly examinations were made during an entire year. Thanks are due to Miss Elizabeth Pearse and Mr. David Palmer who helped with routine observations and in the making of some of the drawings of parasites. Dr. C. F. Korstian identified all woods. Professor F. A. Wolf gave helpful advice at various times and Professor R. F. Poole furnished pure cultures

of three species of wood-rotting fungi. All work on foods was done by Mrs. Patterson and Rankin; that on parasites by Pearse and Wharton.

SEASONAL CYCLES

Though *Passalus cornutus* shows little or no diurnal periodicity, its breeding activities are definitely correlated with changing seasons in the Duke Forest. In the middle of April (1934) some large eggs were observed in the ovaries of females that were dissected. By the middle of May there were a few more and some eggs with brown coats far down in the oviduct were apparently ready to be laid. But at both of these times many ovaries were without large eggs. Throughout June and July eggs were readily collected in the field. Apparently eggs were laid during a period of more than two months, for eggs and larvae of various sizes were present in logs until the middle of August, when pupae appeared. Adults were present at all seasons, but eggs, larvae, and pupae were found only during the warmer months, when temperatures in logs in the forest averaged about 30° C. and air temperatures during the day averaged about 27° C.

Some seasonal variations in the parasites and commensals associated with Passalus in logs were also observed. These will be discussed in detail under the section on parasites. Subelytral and external mites were generally most abundant during cooler months and fewest in summer. Oribatids were found only during July and August. Gregarines, coelomic and enteric nematodes were erratic. The Dexiid fly, *Zelia vertebrata* Say, infested only large larvae and sometimes pupae, and was therefore present during late summer.

FOODS

METHODS

The larvae and adults of *Passalus cornutus* Fabricius used in the writers' experiments were collected from oak logs in various parts of the Duke Forest from June to September, 1935. In a few cases colonies were found in rotting pine, dogwood, and southern shagbark hickory, but never in seasoned woods. Adult beetles tunneled through the entire log but most eggs and larvae were found in the lower parts. The adults required little care in transportation but it was necessary to keep larvae cool and moist.

Several large colonies were kept in the laboratory for observation in aquarium jars or large finger bowls and provided with rotting oak wood in pieces large enough for burrows. Adults from different colonies were kept together but larvae to be kept safely with adults had to be with those from their own colony. Adults and larvae for stock purposes were cared for separately. In any case the wood was changed frequently; chiefly in order to maintain humidity as near optimum as possible.

Under laboratory conditions an adult Passalus weighing approximately 1.5 gms. eats an average of 0.5 gm. of oak wood, or one-third its body weight per day. Presumably this amount would be slightly greater under natural conditions. In the writers' work the following types of food were used: oak-wood agar, sweet potato agar, fungus cultures, midgut contents, seasoned wood, rotting oak-wood sawdust, rotting oak wood prepared by the adults, rotting oak wood sterilized, rotten prepared oak wood sterilized, rotting sterilized oak wood later prepared by adults, and seasoned wood inoculated with various fungi.

Larvae fed on agar, fungus cultures, and midgut contents were kept in petri dishes. These were changed every two or three days. Small larvae fed on various woods were kept in 250 cc. Erlenmeyer flasks. Cork stoppers fitted with glass tubing permitted ventilation without excessive evaporation. Large larvae were kept in finger bowls. A few drops of water were added every two or three days in all cases. Larvae were carefully removed daily from the flasks with tweezers and brushed with a camel's hair brush to remove all particles of dirt. Calipers were used for measuring and an analytical balance for weighing. The larvae were returned to their bottles immediately after being weighed.

All larvae were kept in a room where the humidity, as measured by a psychrometer, varied after the first week between 63% and 83%, and the temperature between 26° and 30° C., except for a week at the end of the experiments when the temperature was as low as 22° C. for two days. Although neither humidity nor temperature was constant, the range was less than that recorded by the Weather Bureau Station in Durham.

It was not possible to keep larvae in flasks as controls because the type of food necessary was not known. The only controls possible were larvae kept in large finger bowls with adults. Portions of the materials from burrows found in the forest were placed with these. Adults fed seasoned wood were kept in bell jars or finger bowls and those in sterilized wood were put directly in 500 cc. flasks in which the wood was sterilized. In these cases also a few drops of distilled water were added every two or three days.

EXPERIMENTS

In the first experiment six larvae ranging in size from 0.038 gm. and 12 mm. to 0.470 gm. and 28 mm. were each placed in 250 cc. Erlenmeyer flasks with only a few drops of water. The information as to how long these larvae would exist without food was desired to determine whether larvae in later experiments were feeding or not. The larvae were weighed and measured every day. One of the six lived two days, three lived three days, one four days, and one five days. Only half of these decreased in length every day

until death while the other three increased the second day and then decreased until death. Weights taken the last day showed an average decrease of 24%.

Sixteen larvae were put on oak-wood agar which was made by adding 25 grams of agar to a liter of liquid strained from boiling oak wood and water. This was done as one means of determining whether food essentials could be obtained from wood alone after destruction of fungi and bacteria, and it was also thought that if the extract did contain enough food it would be in a condition easily accessible. Six of the larvae were hatched on agar. They ranged from 0.02057 gm. and 11.5 mm. to 0.0300 gm. and 12 mm. when put on this medium; while ten others used ranged from 0.1160 gm. and 20 mm. to 1.3748 gm. and 42 mm. These larvae were weighed and measured every day. No newly hatched larva lived more than seven days; four lived three days, and one seven days. They showed an average increase of 19.9% in weight at the last observation. One decreased in length 13.0% before dying; two remained the same; while the three others showed an average increase in length of 7.1%. Of the larger larvae five showed an average increase of 9.91% in weight and a decrease of 0.3% in length. Five showed an average decrease of 15.7% in weight and 11.6% in length.

Attempts were made to feed seven larvae which ranged from 0.0500 gm. and 14 mm. to 0.1500 gm. and 17 mm. pure fungi on agar plates. Three of these were put on *Schizophyllum communa* and four on *Armillaria mellea*. These were weighed and measured only once a week to avoid contamination. Two larvae lived seven days; two, sixteen; two, twenty; and one, twenty-one days. The average increase in weight of all, except the two which lived only one week, was 23.8%; in length, 14.3%.

Twelve newly hatched larvae were fed material taken from the anterior midguts of adults, and weighed and measured daily. It was thought that this food would be the most suitable for young larvae since it would be well broken up and partially digested. The material was changed daily to avoid putrefaction. Larvae ranged from 0.0148 gm. and 10 mm. to 0.0254 gm. and 11 mm. All gained in weight and length remarkably at first but lived only a short while; two lived one day; four, two days; four, three days; one, four days; and one, five days. Two died the day after the experiment began so that no second observation was taken. The average increase in weight for the ten was 56.4%, in length 21.2%.

To test the belief that larvae are not able to exist and grow on sound seasoned wood forty-eight larvae were fed on this food and nothing else. They were weighed and measured every day for two weeks; then every other day. Twenty-four larvae decreased in weight and length before dying with an average decrease of 25.1% in weight and 17.1% in length; thirteen increased in weight and length before dying with an average increase of 33.8% in weight and 13.7% in length; four died the day after the experiment be-

gan; three increased in weight and decreased in length; three decreased in weight but showed no change in length; and one increased in weight and showed no change in length.

Nine large larvae were placed on rotten oak wood which had not been converted into sawdust to see if they would survive and grow. They were measured every three days. The larvae ranged from 0.3860 gm. and 27 mm. to 1.7010 gm. and 42.5 mm., and averaged 1.0458 gm. and 36.7 mm. Five of these became adults, one in thirty-two days, the others between sixty-three and seventy days. The others pupated but died soon after. Another larva died after being kept eighty-one days. One was parasitized by a fly larva and consequently killed.

Forty-three larvae ranging from 0.0209 gm. and 10.5 mm. to 0.4561 gm. and 26 mm. were fed rotten oak wood which had been converted into sawdust. This was done to determine if larvae required small particles of wood, such as that prepared by the adults and because small larvae did not seem able to chew whole rotten oak wood. With twenty-one of these newly hatched larvae wood was used in which no adults had been present. Twenty-four larvae lived two weeks or less, four between two and four weeks, ten between four and eight weeks, three between eight and fourteen weeks, and two between fourteen and seventeen weeks. Four pupated and one became an adult.

Forty-five larvae, including thirty-one newly hatched, and ranging from 0.0147 gm. and 10 mm. to 0.4524 gm. and 26.5 mm. were fed oak wood prepared by the adults, in an attempt to rear larvae from the egg to adult. The newly hatched larvae were measured daily at the beginning of the experiment, but later observed daily and measured every two or three days. Of the forty-five larvae, all increased in weight, one decreased 4.5% in length; twenty-five lived two weeks or less, four lived between two and four weeks, two between four and five weeks, two between eight and ten weeks, eight between ten and fourteen weeks, and one lived seventeen weeks and three days. Six of them became adults and two became pupae and died before becoming mature. Four of the larvae started were injured or eaten by other larvae and are not reported.

Two larvae, one 0.0267 gm. and 11 mm., the other 0.0227 gm. and 10 mm., were kept on rotten oak wood, which had been converted into sawdust and then sterilized. If these larvae had survived it would have eliminated the necessity of the preparation of wood by the adults, of the presence of fungi at the time of feeding, or the presence of living bacteria. The larvae were weighed and measured daily. One larva lived three days, the other seven. Since only two larvae were used in the experiment no definite conclusions can be drawn.

Thirteen larvae, ranging in size from 0.0183 gm. and 9 mm. to 0.0296 gm. and 11 mm. were kept on rotting oak wood prepared by the adults and then

sterilized. This was to determine if fungi or bacteria in the wood were necessary in the food. The larvae were measured and weighed every other day. All but one larva increased in weight and length. Three lived a week or less, five between one and two weeks, and four between two and three weeks (Table 1).

TABLE 1. Behavior of larvae fed on oak wood prepared by adult beetles and sterilized.

Beginning of expt.		End of expt.			Per Cent Increase	
Weight grams	Length mm.	Weight grams	Length mm.	Days of Life	Weight	Length
0.0183	9	0.0352	12	7	92.34	33.33
0.0296	11	0.0366	13	8	23.64	18.18
0.0288	11	0.0325	12	2	12.84	9.09
0.0272	11	0.0350	11	10	28.67	0
0.0266	11.5	0.0700	17	33	163.15	47.82
0.0231	11	0.0440	14	16	90.47	27.27
0.0236	12	0.0465	14	20	97.03	16.66
0.0236	11.5	0.0355	13	14	50.42	13.04
0.0200	10	0.0415	14	19	107.50	40.00
0.0238	11	0.0317	12	13	33.19	9.09
0.0253	11	0.0441	12.5	17	74.30	13.04
0.0252	11	0.0350	11.5	13	38.88	4.54
0.0214	11	0.0214	11	6	0	0

Four larvae were put on rotten, sterilized oak wood later prepared by adults, and weighed and measured every day. If larvae on rotten unprepared sterilized oak wood had died and these had lived, it would have shown that the adults in preparing the wood had changed it in such a way that it then had something necessary for life and growth. One larva lived six days, two seven days, and one ten days. All increased in weight and length before dying (Table 2).

TABLE 2. Behavior of larvae on oak wood prepared by adults.

Beginning of expt.		End of expt.		Days of life	Per Cent Increase	
Weight	Length	Weight	Length		Weight	Length
0.0274	12	0.0365	13.5	7	33.21	12.50
0.0278	12	0.0302	12.5	7	8.63	4.16
0.0295	12.5	0.0379	13	10	28.47	4.00
0.0275	11	0.0379	12.5	6	37.81	13.54

Five sets of experiments were tried in which fungi were allowed to act on sterilized, seasoned, sound oak wood for a definite period of time. The wood was then sterilized and inoculated with the larvae to see if they could complete the digestion of the wood which had been started by the fungus. Sterile sweet potato agar was added to the wood so that the fungi would grow more quickly. In the first case the fungi used were allowed to grow for seven

days, and three larvae were then introduced. These were weighed and measured only once a week in order to avoid contamination. The woods and fungi

TABLE 3. Behavior of larvae fed on oak wood on which fungi (Schizophyllum) were growing.

Wood	Beginning of expt.		Days of life	End of expt.		Per cent increase or decrease	
	Weight	Length		Weight	Length	Weight	Length
Post oak	0.1800	20	43	0.2302	22	27.88	10.00
Black oak	0.1770	22	48	0.2540	24	43.50	9.09
Southern red oak	0.3000	25	18	0.2623	23	—12.56	—8.00

used and the record of larvae are given in Table 3. In another experiment the fungi used were allowed to grow for sixteen days and five larvae were then introduced. Table 4 shows the results. In a third experiment the fungi were

TABLE 4. Behavior of larvae fed on oak wood and fungus.

Wood	Fungus	Beginning of expt.		Days of life	End of expt.		Per cent increase or decrease	
		Weight	Length		Weight	Length	Weight	Length
Black oak	Polyporus	0.4461	28	69	0.5860	30	31.36	7.14
Southern red oak	Schizophyllum	0.4021	28.5	15	0.2500	20	—37.82	—29.82
Post oak	Polyporus	0.5800	32	69	0.5281	28	— 8.94	—12.50
Post oak	Schizophyllum	0.7328	35	69	0.8025	34	9.51	— 2.85
Black oak	Schizophyllum	0.5784	31	40	0.5586	30	— 3.42	— 3.22

allowed to grow for twenty-two days. Two larvae were introduced (Table 5).

TABLE 5. Behavior of larvae fed on oak wood and fungus (Armillaria).

Wood	Beginning of expt.		Days of life
	Weight	Length	
Black oak	0.9302	36	Pupated in 18 days, died 74 days
Post oak	1.2573	42	Pupated in 13 days, died 79 days

In a fourth experiment fungi were allowed to grow for twenty-three days and four larvae were then introduced (Table 6). In a fifth experiment the

TABLE 6. Behavior of larvae fed on oak wood and fungus.

Wood	Fungus	Weight	Length	Length of life
Black oak	Polyporus	1.0140	36	Pupated, 21 days. Died 29 days
Southern red oak	Schizophyllum	1.0181	36	26 days
Post oak	Polyporus	0.9750	37	Pupated, 13. Adult 27
Post oak	Schizophyllum	1.0138	36	68 days

fungi were allowed to grow for thirty days. Three larvae were used (Table 7). Fourteen of all the larvae fed on wood and fungus died before pupating; the remaining five pupated or became adults and then died.

TABLE 7. Behavior of larvae fed on oak wood and fungus.

Wood	Fungus	Weight	Length	Days of life
Black oak.....	Schizopyllum.....	0.9791	36	51
Post oak.....	Polyporus.....	0.6158	28	7
Black oak.....	Polyporus.....	1.0950	38	Pupated 17, died 29 days

To be sure that adults could not survive on seasoned woods, 48 were kept on seasoned woods which had not been broken up at all. The following woods were used: red cedar sapwood, red cedar heartwood, black gum, red gum, white ash, loblolly pine, shortleaf pine, southern shagbark hickory, mockernut hickory, mulberry, white oak, post oak, black oak, southern red oak, dogwood, and sourwood. Ten of the beetles lived a week or less, thirteen lived between one and two weeks, ten lived between two and three weeks, six lived between three and four weeks, one lived between four and five weeks, one between six and seven weeks, and one sixteen weeks. Later eight adults were put on seasoned southern red oak which was cut up and partly converted into sawdust to eliminate the possibility that the adults in the preceding experiment died because of inability to chew the seasoned wood. Two died after eleven days, one died in seventeen days, and the other five died in thirty-eight days.

Nine adults were kept on sterilized rotten oak wood. One died after twenty-nine days, one after fifty-seven days, while the seven others died after one hundred-sixty-eight days. Two adult beetles were kept in flasks with all conditions the same except that the food in this case was plain rotting oak wood. Both lived and were active throughout the experiment (168 days). When a beetle was placed in sterilized wood it may have introduced bacteria, but it probably did not introduce fungi. No fungi could be obtained from beetle gut-contents (adults) plated on agar, nor did visible mycelia grow in the inoculated wood. In other experiments inoculation of sterilized wood with fungi produced visible mycelia within a very short time.

Four colonies were kept in wood for observation. In the first, two adults were kept with two larvae and nine eggs. The two original larvae lived for forty-seven days, but both were finally destroyed, evidently by the adults. Three of the eggs hatched but the larvae from them were also killed. In the second colony eight larvae were kept with two adults. All of these also were destroyed either by the adults or by other larvae. At different times adults and large larvae were seen to kill small larvae from the same colony. In the third colony four larvae were kept but all were parasitized and consequently died. In the fourth colony also, in which eight larvae were kept with adults,

the larvae were all parasitized. However, in another large colony which was kept in a large aquarium jar with no particular attention, larvae hatched and developed to adults. Consequently it seems safe to assume that larvae would have lived under the same conditions as the experimental larvae and thus have served as controls if they had been given proper food.

Discussion of Foods and Nutrition

Oak wood agar made up as described (p. 461) was not an adequate diet for Passalus larvae. Either it contained insufficient wood or it did not provide enough roughage, for later experiments showed that the same sort of wood was suitable for other larvae. Pure fungus did not contain all food essentials, as results on seven larvae fed it indicate. It took many more larvae to get favorable results in other experiments so that the small number here may have vitiated the results. However, other experiments point to the conclusion that wood is absolutely necessary. It is a question why no larva survived more than five days on midgut contents from adult beetles since that food was well broken up and partially digested. The larvae ate voraciously and increased remarkably in weight and length before dying in this experiment. Perhaps the food was too rich. Seasoned wood was not very suitable for food. One larva did live one hundred-eleven days on seasoned black gum and increased 124.77% in weight and 46.42% in length before dying, but it must have been exceptionally hardy. All others died much sooner.

All food essentials necessary for the development of Passalus larvae are present in rotting oak wood. Newly hatched larvae did not grow and pupate unless the wood was prepared by the adults. Larvae as small as 0.0300 gm. require wood that has been converted into sawdust. Even then it is difficult to rear them. This indicates that converting wood into sawdust in the laboratory does not render the wood as available as that prepared and left in mines as frass by adults. After reaching a weight of approximately 0.3800 gm., hardy larvae may metamorphose and become adults on rotten oak wood which has not been converted into sawdust. Such larvae have jaws strong enough to break up the wood, independently of the adult.

Experiments in which larvae were fed rotting oak wood prepared by the adults and then sterilized appear to indicate that the presence of fungi or bacteria in the wood at the time of feeding is necessary. However, larvae which were fed seasoned wood on which fungi had acted for thirty days and which was then sterilized, did metamorphose. In this case the presence of fungi or bacteria was not necessary. The larvae were of course larger when the experiment began. It seems logical to suppose that if a greater number of larvae had been fed rotting oak wood prepared by the adults and then sterilized, some would have metamorphosed. Adults have been kept for twenty-four weeks on sterilized rotten oak wood. They are as active as the controls,

thus substantiating the belief that the food essentials are found in rotten oak wood alone. Living fungi or bacteria do not appear to be necessary as ingredients of the food of adult Passali.

All adults which were raised in the laboratory were smaller in size than those found in the forest. It should be mentioned also that the rate of growth of larvae in the laboratory was noticeably less than that of those observed in the field. Unfavorable humidity conditions may have been responsible for such differences.

It would be desirable to rear more newly-hatched larvae on seasoned wood on which fungus has acted for certain periods of time before being sterilized, as in the experiments described. This would prove conclusively: (1) that the food essentials for larvae are in either rotted oak wood with the living fungi and bacteria or in rotted oak wood alone, and (2) how long fungi must act on the wood before it can be used as food.

There has been much discussion concerning the food requirements of insects which live in wood. Uvarov (1928) after an extensive review says:

> It is known that the nutrition of the vast majority (perhaps of all) wood-feeding insects is intimately connected with their symbiotic micro-organisms, but the physiological side of their nutrition remains entirely unknown. Indeed all that is known is that the insects apparently feeding on wood, are not using wood directly as food. There is, however, no evidence at all as to what substances they do, in fact, feed on; these may be particles of wood partially digested by micro-organisms, or their secretions, or even the micro-organisms themselves. In other words, wood-eating insects must be classified as insects of absolutely unknown feeding habits.

There is no question that fungi produce a variety of enzymes which are capable of digesting lignin, cellulose, and other rather indigestible organic substances (Zeller, 1916). They are also known to contain Vitamin B (Gorcia, Peterson, and Steenbock, 1936), which is essential for the nutrition of many insects. Fungi are often found within insects and some types may have elaborate mechanisms for passing from one host to another (Schrader, 1923; Schwartz, 1932). Payne (1931) has shown conclusively that a particular fungus, *Armillaria mellea* Vahl., is necessary in the food of certain beetle larvae which live in oak bark. The beetles in question are usually annuals, but when fed on sterilized oak bark the larvae remained alive for as much as ten years without pupating. However, when a little unsterilized wood or fungus was added to the diet, the larvae pupated and the life cycle was completed in a short time.

In termites Hendee (1933, 1934) found no specific relation between particular species of fungi and nutritional requirements, although she isolated fifteen species of fungi from termites and showed that the insects are the primary agents in inoculating wood with fungus spores. Cleveland (1934) has accumulated considerable evidence to show that flagellate protozoans in

termites and blattids digest cellulose and convert it into soluble products like dextrose which are assimilated by the insect hosts. Mansour and Mansour-Bek (1934) do not altogether agree with Cleveland's findings. They studied the larvae of two cerambycid beetles and found that one was able to digest cellulose and that the other depended on sugars and starches present in wood; neither contained micro-organisms. These men believe that insects which contain micro-organisms utilize them directly as food and do not assimilate the wood or other food which the organisms digest for their own needs. In certain lamellicorn larvae bacteria appear to be the chief agents in breaking up cellulose in the intestine (Wiedemann, 1930).

No protozoans have been observed to be regularly present in the alimentary tract of *Passalus cornutus*. There are at times gregarines in the midgut, but these probably play no important rôle in nutrition. The larva of this beetle apparently belongs to the class of insects which live on rotten wood which contains fungi. Very young larvae apparently also require something that the adult beetles add to rotten wood in chewing it and passing it through the gut. Larger larvae flourish on rotten wood that has not even been finely divided and which has been sterilized. Living fungi or bacteria are not essential in the food of adult Passali.

PARASITES AND COMMENSALS

METHODS

Passalus cornutus was collected from several localities in North Carolina at various seasons to examine its parasites and commensals, after which a more thorough and systematic survey was undertaken. A particular area, entered from Gate 10 in the Duke Forest, was visited each month for an entire year. At least ten beetles were collected on each field trip, five from logs on a hillside and five from logs at the base of the same hill near a small stream. These were placed at once in separate rubber-stoppered bottles and carried to the laboratory. No significant differences in parasites and commensals was observed between those from the higher, dryer regions and those from the lower, moister valley.

Collecting bottles were kept in a cold room at 4° C. They were removed singly for examination within two days. No beetles died before being studied. Each was carefully searched for external parasites; the cork and inside of the bottle were carefully examined with a binocular microscope. Nothing but mites was found on the outside of the beetles. Wings and legs were then removed, placed in a petri dish with the body of the beetle and all parts were again examined under a binocular microscope. Mites were removed, counted, and preserved. The body was then placed on a glass plate and dissected under a binocular microscope. Clean water was added from a dropper at intervals while the dissection was in progress. This kept the internal organs

from drying up before the small animals in them could be counted. The following annotated list describes the animals found and gives relevant information concerning them.

Phylum Protozoa
Class Sporozoea
Subclass Telosporidia
Order Gregarinida
Suborder Eugregarina
Legion Cephalina

Gregarina passali-cornuti Leidy

This gregarine was always found in the midgut, where it was attached to the wall or at times free in the lumen. During the year when routine monthly examinations were made no particular seasonal periodicity was observed. In June three lots of ten each from three different localities were

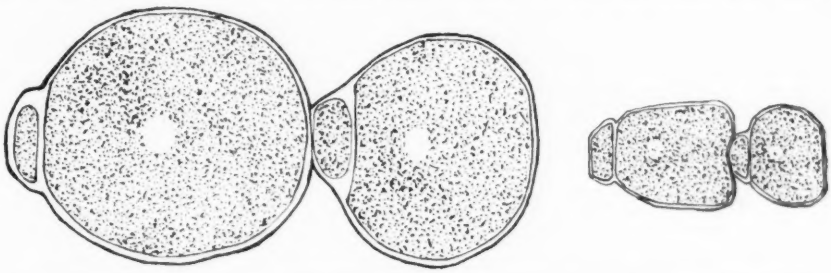


FIG. 2. *Gregarina passali-cornuti* Leidy: two pairs of individuals. The line indicates one millimeter.

examined. Among these six individuals from one lot contained gregarines, and none was found in the other two lots. Among the ten examined each month from the selected locality in the Duke Forest the following figures give the number of beetles infested and the average number of gregarines per individual: January, 1—1.8; February, 1—0.3; March, 1—2.0; April, 0.0; May, 0.0; June, 4—6.1; July, 0.0; August, 0.0; September, 0.0; October, 0.0; November, 2—9.6; December, 2—4.2; average 0.9—1.7.

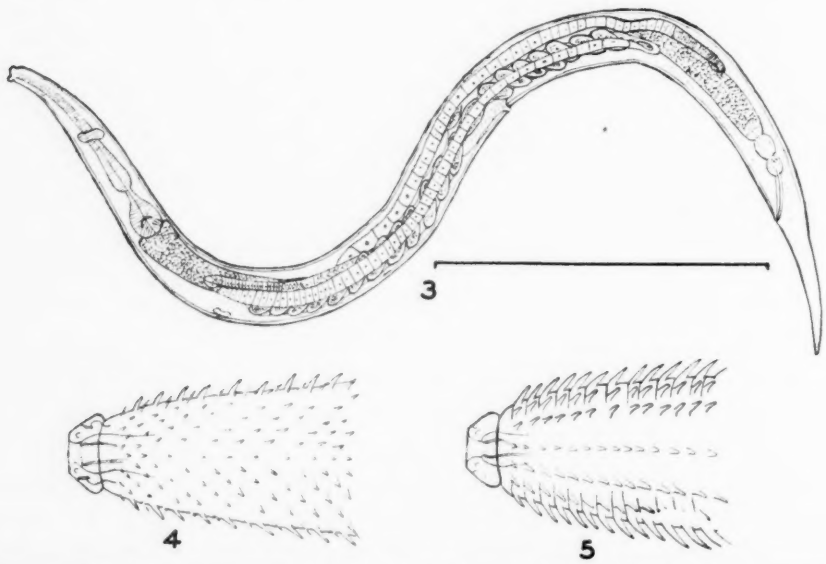
Phylum Nematoda
Class Phasmidea
Order Rhabditida
Family Rhabditidae
Subfamily Thelastomatinae

Histrignathus rigidus Leidy

This parasite lives in the anterior end of the pyloric section of the enteron. Christie (1934) has described two forms of this nematode, which differ in the number and arrangement of dermal spines. These have been called *H. rigidus*

Leidy and *H. histrix* (Cobb). As they occur together in *Passalus cornutus* they are perhaps merely forms of one species and the writer therefore uses the earlier name, though both occur in the beetles in the Duke Forest. Christie says "there is the possibility that we are dealing, not with 2 species, but with a single, polymorphic species in which occur 2 types of females and 1 type of male."

This nematode was found during every month in the year, with the largest numbers in April, July, August, and November and the smallest numbers in February, June, and September; so there appears to be no significant variation correlated with different seasons. The number of beetles infested and the average number of parasites per host in the ten beetles examined each month were as follows: January, 6—3.5; February, 3—1.5; March, 8—3.9; April, 8—8.7; May, 8—6.1; June, 2—2.6; July, 7—5.6; August, 8—5.9; September, 5—1.0; October, 5—3.7; November, 7—8.8; December, 2—1.2; average, 5.4—4.4.



FIGS. 3-5. *Histrignathus rigidus* Leidy; after Christie (1934): 3, female; 4, anterior end of *H. histrix* form; 5, anterior end of *H. rigidus* form.

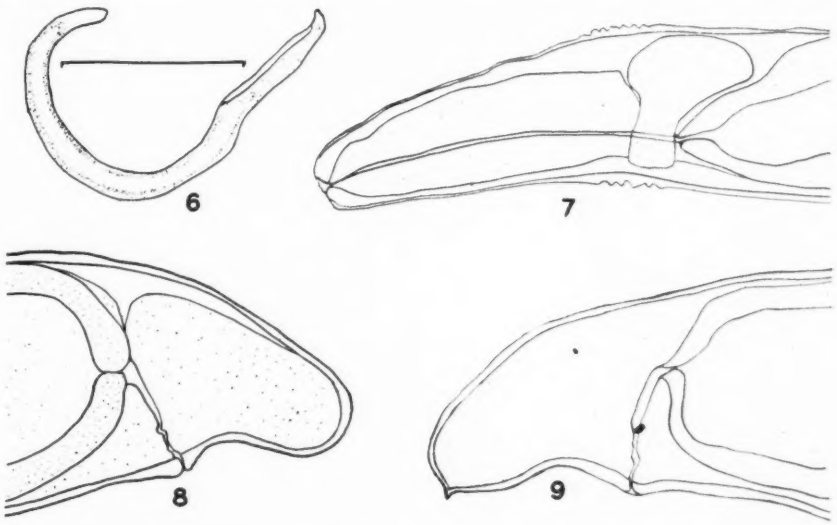
Chondronema passali (Leidy)

This nematode lives in the body-cavity of Passalus. Christie and Chitwood (1931) have made an extensive study of the parasite. They say:

The parasites enter the host as very young larvae. That the beetles are being continually infected is indicated by the fact that very young parasites are present regardless of the age of the beetles or the time of the year when they are collected. It seems to us probable that the larval parasites are taken per os while the beetles are feeding. The exceedingly heavy infestations encountered suggests the possibility that the mother nemas may be swallowed. . . . Whenever beetles were killed and placed in cultures of moist, decayed

wood, all the body-cavity parasites died, which seems to render the possibility of the parasites being liberated through the death of the host unlikely. The oldest of the body-cavity parasites were on many occasions removed from the beetles and placed in moist decayed wood and various other types of cultures, but they always died. . . . We therefore concluded that . . . the adult nemas live free in moist, decayed wood or frass; and, after many hours of tedious searching of such material, we finally discovered the adult nema.

This species, as judged by our routine monthly examinations in the Duke Forest increases greatly in numbers in late summer. This is probably due to the fact that after September there are many beetles which have recently emerged from pupae and have not yet become infested or contain only a few worms. During the summer the degree of infestation steadily increases and reaches a maximum average just before the new brood of a year begins to



FIGS. 6-9. *Chondronema passali* (Leidy): 6, side view of worm from body cavity; 7, anterior end; 8, posterior end without spine; 9, posterior end with spine.

emerge, but an individual may continue to accumulate worms throughout its life. In one instance about 4,260 were counted in a single beetle (August). The number of beetles infested in each month and the average number of parasites per host were as follows: January, 10—57.7; February, 10—95.6; March, 10—68.1; April, 10—133.0; May, 9—79.5; June, 10—228.1; July, 10—324.0; August, 10—1,028.0; September, 10—3,274.7; October, 7—46.3; November, 9—140.5; December, 10—130.8; average, 9.6—467.2.

Phylum Arthropoda
Class Arachnida
Order Acarina

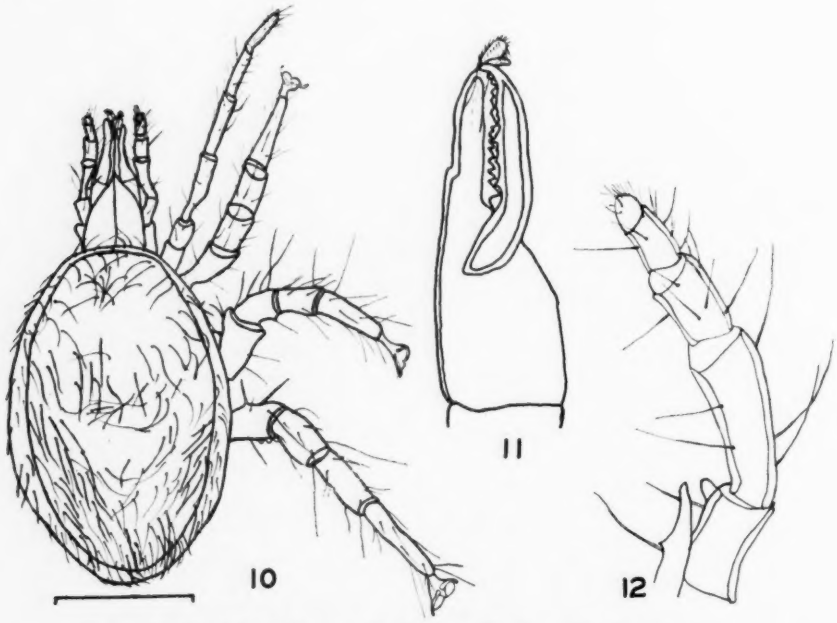
The seasonal occurrence of all species of mites found associated with *Passalus cornutus* is shown in Table 8. In studying these mites much

help was received from Dr. H. E. Ewing who examined our material and loaned specimens from the United States Museum for comparison. All new species in this paper were described by A. S. Pearse and G. W. Wharton and have been examined by Dr. Ewing.

Suborder Parasitina
Family Parasitidae
Subfamily Parasitinae

Megisthanus floridanus Banks

This large, flat mite was never abundant and at times none was collected from the ten Passali which were examined each month. It ran freely over the surface of its host, and was never found beneath the wings. This species is readily recognized by the strong teeth on the posterior borders of the hind femora.

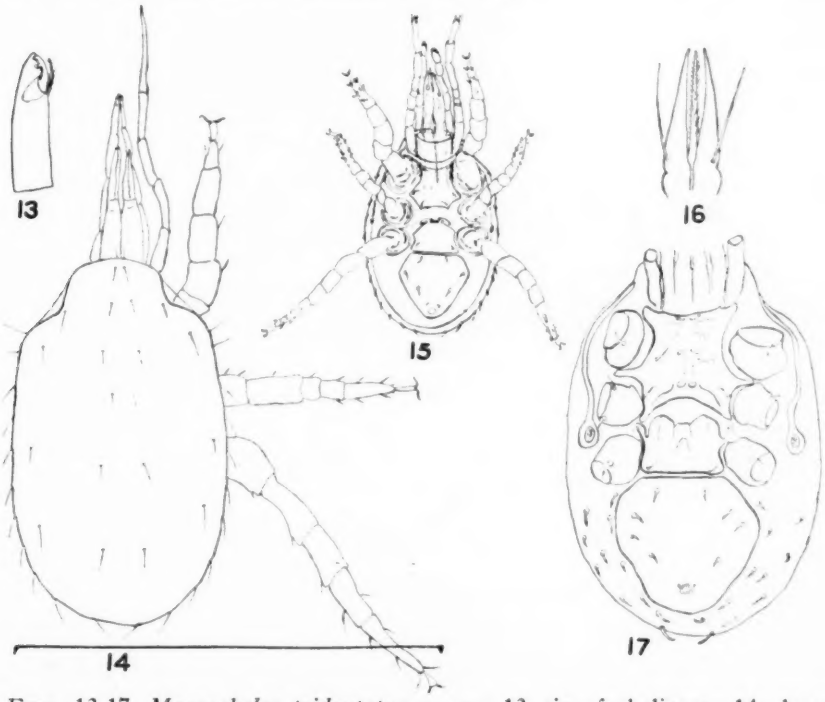


FIGS. 10-12. *Megisthanus floridanus* Banks: 10, dorsal view; 11, tip of chelicera; 12, pedipalp.

The body is oval in outline, the anterior sixth sharply constricted; both ends rounded; length 0.83 mm.; width, 0.52 mm., of the constricted anterior sixth, 0.23 mm. On the anterior margin are two delicate setae; behind these there are four rows of four small setae across the dorsum and a pair near the middle; along the lateral margins are eleven pairs of setae. The ventrum has three median plates; sternal, genital, and ventro-anal; these bear setae as follows: 6, 4, 10. The male genital aperture is in front of the sternal plate; the female aperture in front of the genital plate between the bases of the third legs.

Macrocheles tridentatus n. sp.

The chelicerae are chelate; the dactyl bears two blunt, rough, recurved teeth on its distal half and has a curved tip; the fixed finger has a stout tooth near its tip; a plumose hair stands at the base of the dactyl. The pedipalpi are 5-segmented; in order of length the segments rank: 5, 4, 2, 3, 1; all are somewhat setose and there is a group of small setae at the tip of segment five. The hypostome bears two setae; a median, tapering setose process; and two slender, pointed, lateral teeth. The legs are all shorter than the body; in order of length they rank: 4, 1, 3, 2; each is setose and the last three also bear a pair of spines and a caruncle at the tip.



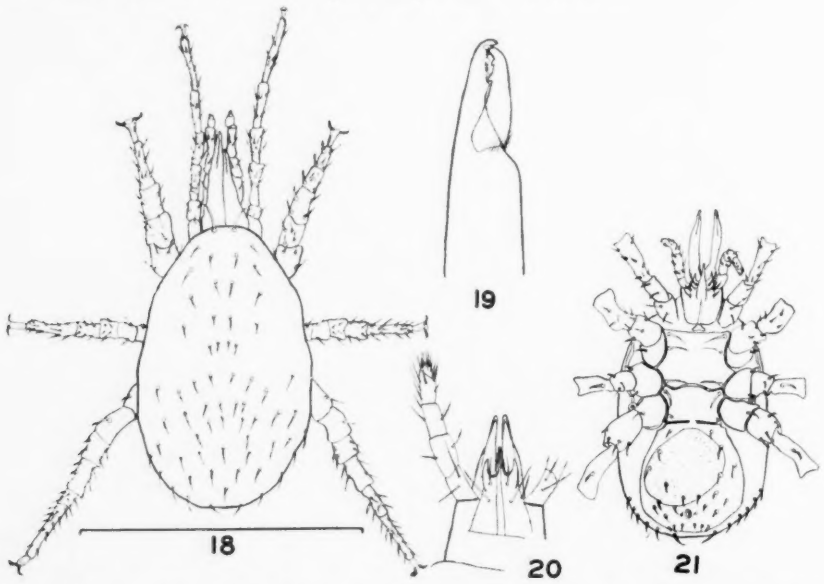
FIGS. 13-17. *Macrocheles tridentatus* n. sp.: 13, tip of chelicera; 14, dorsal view; 15, nymph; 16, mouth parts; 17, ventral view of female.

Types, male and female (U. S. Nat. Mus. No. 1172): on *Passalus cornutus* Fabricius, Duke Forest, Durham, N. C.; June 7 and September 17, 1933; respectively; Collector, A. S. Pearse. The specimen is named for its trident hypostome.

The body is almost 1 mm. long, oval in outline and somewhat truncate at each end. The dorsum bears about fifty rather stout setae; there are ten to fourteen more setae along the posterior margin and two at the anterior end; the antero-lateral regions are without setae. The ventrum has three plates: sternal, gental, and ventro-anal, which bear setae as follows: 6, 4, 28. The male genital aperture is in front of the sternal plate; the female aperture is in front of the genital plate.

Sciodes trifidus n. sp.

The chelicerae are chelate; the dactyl bears two blunt teeth on its distal half and has a curved tip; the fixed finger has about thirteen small teeth near its recurved tip. There is a transverse row of setae at the base of the dactyl on the palm. The pedipalpi are 5-segmented; in order of length the segments are: 4, 3, 1, 2, 5; all are somewhat setose and there is a group of setae at the tip of Segment 5. The hypostome bears four ventral setae and ends in a trident (hence *S. trifidus*); from its dorsal surface a conical setose tooth projects anteriorly. The legs each bear two claws and a caruncle; they are well armed with stout setae; in order of length they rank: 1, 4, 2, 3.



FIGS. 18-21. *Sciodes trifidus* n. sp.: 18, dorsal view; 19, tip of chelicera; 20, hypostome, tip of chelicera, and pedipalp; 21, ventral view of female.

Type (U. S. Nat. Mus. No. 1179): on *Passalus cornutus* Fabricius, Duke Forest, Durham, N. C., June 27, 1933; Collector, A. S. Pearse.

Mites belonging to this species usually rested in the spaces between the legs or between the body regions of Passalus. When disturbed they ran rapidly about over their hosts.

Caelenopsis latus Banks

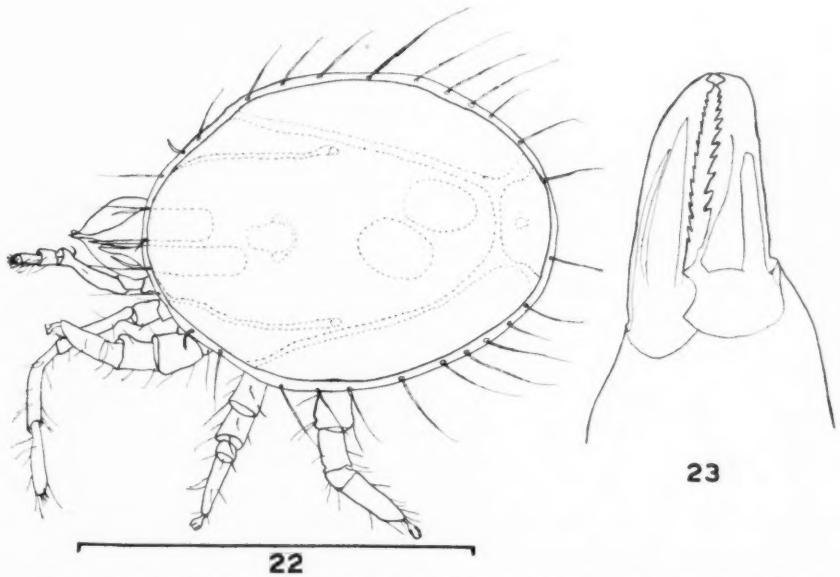
This species is peculiar among those which occur on Passalus, in having clearly defined and separate ventral, lateral, and anal plates. It was somewhat more common in autumn than at other seasons. Its distribution and behavior on the body of its host were about the same as those of the last species.

Passalacarus n. gen.

Parasitinae. The first legs are without caruncles or claws, and thus agree with those in the genera Podocium, Rhodocarus, Caelenopsis, Euzercon, Macro-

cheles, Megisthanus, and the Antennophori. The dorsal shield is undivided, as in the last four genera mentioned. The ventrum shows lateral plates and thus agrees with Euzercon and Caelenopsis. Passalacarus is distinct from the short-legged Antennophori, for the representatives of the new genus have legs considerably longer than the width of the body. It most closely resembles Macrocheles, but differs from that genus in the following characters: the dorsum is setose at the margins and toward the posterior end, but bears few setae on the middle and anterior surfaces; the shape of the body is oval with the posterior end pointed in both sexes; the fused anal and ventral plates are thus elongated and tapering posteriorly; the chelicera has a flat, jointed appendage and a plumose seta at the base of its dactylus; the hypostomal plate bears a semicircular disc with radiating setae below, four stout spines, and a terminal conical process with two setae at its tip.

Type Species: *P. sylvestris* Pearse and Wharton.

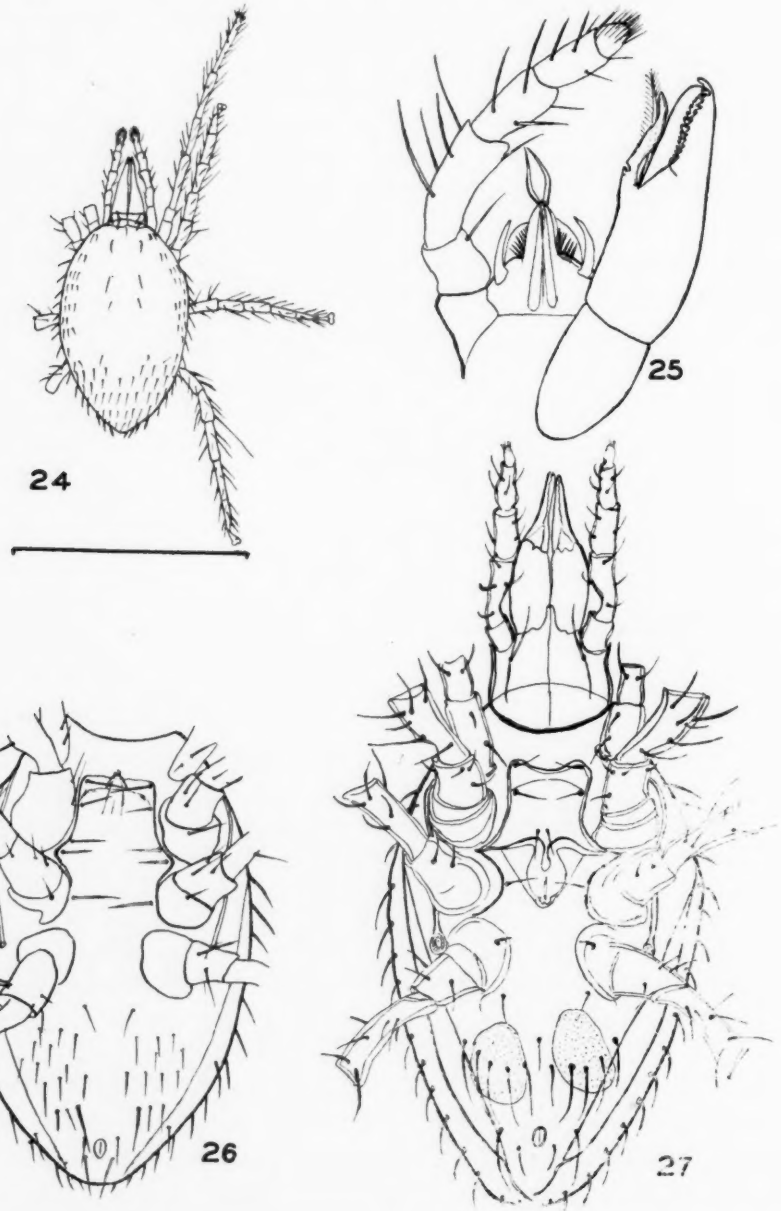


FIGS. *22-23. Caelenopsis latus* Banks: *22*, dorsal view; *23*, tip of chelicera.

Passalacarus sylvestris n. sp.

The body is conical, tapering somewhat toward the posterior end; 0.90 mm. long, 0.54 mm. wide. The dorsum is flat, but slightly elevated; with 36 setae around the margin of the posterior three-fourths, four complete and two partial transverse rows in the posterior third, nine transverse groups of one to three along each margin, three pairs along the median line on the anterior half, one median seta on the anterior margin. The ventrum shows a large median plate and two slender marginal plates in the posterior two thirds. There are two (♀) or four (♂) transverse rows or setae on the posterior third and two pairs on the anterior half there are four or five pairs. The

male genital aperture is in front of the sternal plate; that of the female is between the bases of the third legs. The stigma is opposite the coxa of the fourth legs and the peritreme curves forward around the base of the first leg. The eggs within the female are ovate; 0.16 mm. long.



FIGS. 24-27. *Passalacarus sylvestris* n. sp.: 24, dorsal view; 25, pedipalp, hypostome, and chelicera; 26, ventral view of male; 27, ventral view of female.

The chelicera (Fig. 25) is 2-segmented; the movable dactyl is toothed on its inner margin and hooked at its tip; at its base the palm is produced into a flat, jointed appendage and bears a plumose seta; the dactyl is less than half

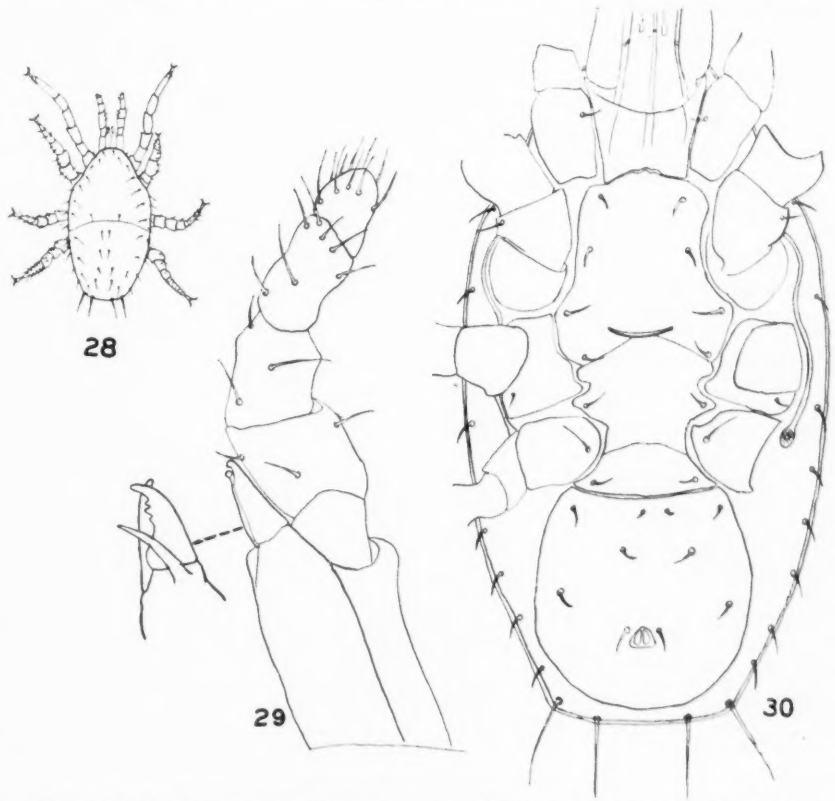
as long as the basal segment. The pedipalp is 5-segmented; the first segment is less than half as long as the second; the third is two-thirds as long as the second; the fourth, slightly shorter than the third; the fifth half as long as the fourth and setose; the pedipalp is also sparsely setose throughout the segments from base to tip bearing the following numbers of setae: 1, 5, 4, 5, 20. The hypostome is as described under the genus. The legs are setose; the first is longer than the body and bears no caruncles and two claws; the second and third are nearly equal and shorter than the fourth.

Types, male and female (U. S. Nat. Mus. No. 1175) Duke Forest, Durham, N. C., May 19, 1934 and August 19, 1933, respectively; on *Passalus cornutus* Fabricius; A. S. Pearse, Collector.

In the Duke Forest this species occurred in maximum numbers in the autumn (Table 8). It was always found on the outside of Passalus.

Zercon passsalorum n. sp.

The body is elongated, oval in outline, tapered and rounded at the anterior and truncated at the posterior end; length, 0.31 mm.; width, 0.17 mm. There are four stout setae on the posterior border; ten setae along each lateral margin, and eleven on the dorsum near the margin. The dorsum is divided into approximately equal anterior and posterior halves by a transverse groove. There are five pairs of setae along the median line behind the groove and



FIGS. 28-30. *Zercon passalorum* n. sp.: 28, dorsal view; 29, chelicera and pedipalp; 30, ventral view of male.

another just anterior to it. The ventrum of the male shows two median plates, a sterno-genital plate between the legs, and a ventro-anal plate behind. There are six pairs of setae along the lateral margins of the former and ten on the latter. The stigma is opposite the fourth coxa and the peritreme follows a sinuous course forward. The male genital aperture is a curved transverse slit in the middle of the sterno-genital plate. The female has a large ventro-anal plate which occupies most of the space behind the posterior pair of legs.

The chelicerae are chelate; the dactyl is about a fourth as long as the basal segment; it bears three teeth on its distal half. A conical curved process arises from the basal segment at the base of the dactyl. The pedipalp is 5-segmented; the second segment is longer than the first; the second, third and fourth grow progressively a little longer; the terminal segment is about half as long as the fourth, and setose. The legs each terminate in a caruncle and two claws; they bear short setae throughout, except the first pair which are setose only on the tarsus; from longest to shortest they may be arranged in the following order: 1, 4, 3, 2; the first leg is slightly shorter than the length of the body.

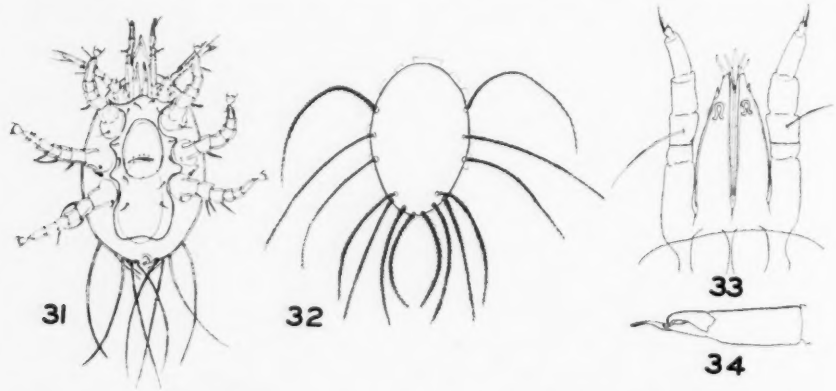
Types, male and female (U. S. Nat. Mus. No. 1173): Duke Forest, Durham, N. C.; August 19, 1934; under wings of *Passalus cornutus* Fabricius; A. S. Pearse, Collector.

This species was common the year round under the wings of Passalus and the numbers increased greatly in the winter (Table 8).

Subfamily Uropodinae

Uroseius quercus n. sp.

The body is oval in outline; both ends rounded; tapering a little anteriorly; flat; length, 0.42 mm.; width, 0.27 mm. On the dorsum along the middle third of each side are three plumose setae which are slightly longer than the body; across the posterior margin are eight slightly shorter plumose setae. The anterior margin projects over the bases of the mouth parts and the first pair of

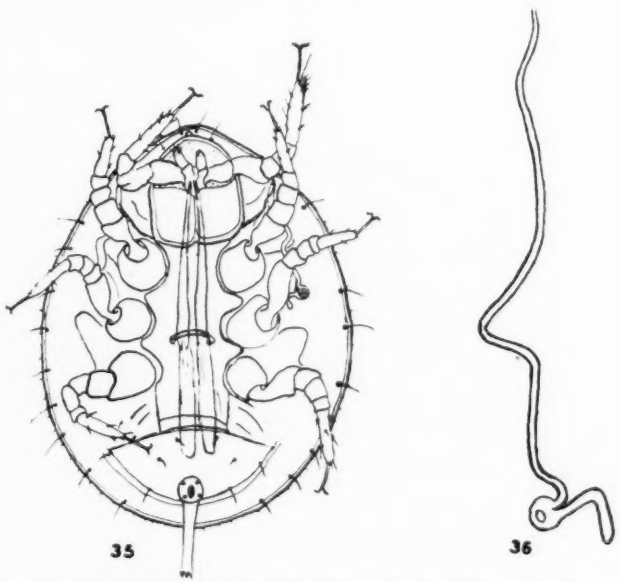


FIGS. 31-34. *Uroseius quercus* n. sp.: 31, ventral view; 32, dorsal view without appendages; 33, ventral view of mouth parts, 34, chelicera.

legs. The ventrum bears six short hairs at the anterior margin in two longitudinal rows close to the bases of the coxae. The anus is on the posterior margin. The female aperture is a slightly curved transverse slit between the bases of the third legs. The male aperture is in front of the bases of the first legs between a pair of conical, anteriorly directed processes on the sternal plate. The stigma is opposite the anterior border of the base of the fourth leg; the peritreme is very short and straight.

The chelicera is chelate; on the inner margin of both the fixed finger and on the dactyl is a poorly defined tooth near the curved tip; the dactyl is about a third as long as the basal segment; a conical process arises near the base of the fixed finger and extends beyond the tip of the segment. The pedipalpi are 5-segmented; the segments increase progressively in length to the fifth, which is about as long as the first and setose; the second segment bears a single long seta. The hypostome is elongated and made up of two conical processes, each of which bears a horse-shoe shaped sculpture near its tip; distal to these marks are two stout acute lateral spines. The legs are short; the first pair are without caruncles or claws; according to length they rank in the following order: 4, 3, 2, 1; the fourth leg is slightly less than the width of the body; the legs are sparsely provided with plumose and naked setae.

The larva has long setae on its legs as well as its body; those on the body are limited to four along the posterior border.



FIGS. 35-36. *Uroobovella setosa* n. sp., nymph: 33, ventral view; 34, left peritreme.

Types, male and female (U. S. Nat. Mus. No. 1174): Duke Forest, Durham, N. C.; August 18, 1933 and May 19, 1934; on *Passalus cornutus* Fabricius; A. S. Pearse, Collector.

This little mite is usually found on the outside of Passalus, where it lurks in the crevices between the parts near the anterior end, but sometimes it creeps under the elytra. It is very slow in its movements. This fact and the very long setae on its body make it easy to recognize. It occurred in considerable numbers throughout the year on Passali in rotting logs in the Duke Forest.

Uroobovella setosa n. sp.

Only attached nymphs were collected. The adults are probably free-

living. The body is flat and oval in outline; length, 0.57 mm.; width, 0.44 mm. The dorsum is rough, pitted and finely tuberculate; without setae. The ventrum has a thickened rim around the margin; impressed foveae for the legs, and well defined anal and ventral plates; setae around the whole margin; and a camerostome which receives the first legs and mouth parts when retracted. The slender chelate chelicerae are about 5/8 as long as the body; the dactyl less than 1/12 as long as the basal segment when retracted within the body. The pedipalp is short; the segments fall in the following order according to length: 4, 1, 2, 3, 5; the tip is setose. The legs all bear a pair of claws and a caruncle at their tips; the tarsi are somewhat pedicellate, with a few short setae, the first pair more than the others. The legs are about equal in length. The stigma is slightly anterior to the third pair of legs. The peritreme is slender with a short, curved, posterio-median branch and a very sinuous anterior trunk extending forward beside the camerostome.

Type (U. S. Nat. Mus. No. 1177): Duke Forest, Durham, N. C.; August 14, 1933; on *Passalus cornutus* Fabricius; Collector, A. S. Pearse.

This nymphal mite with other species of uropodids was commonly found attached by anal filaments in the cavities on the ventral side of the head of Passalus. It was less common than the next species.

Uroobovella spinosa n. sp.

Only nymphs have been collected. The body is oval in outline slightly tapered anteriorly; length, 0.37 mm.; width, 0.23 mm. The foveae for the reception of the legs are deeply impressed into the ventrum and the marginal thickening is heavy. Along the margin are about twenty pairs of curved spinose setae. The anterior margin projects over and conceals the retracted mouth parts and first legs in the camerostome; it is truncate and bears two curved setae. The sternoventral plate is constricted between the bases of the fourth legs, there are three pairs of small setae in front. The anal plate is almost round and bears three pairs of small setae. The stigma is lateral to the bases of the third legs. The peritreme is sinuous.

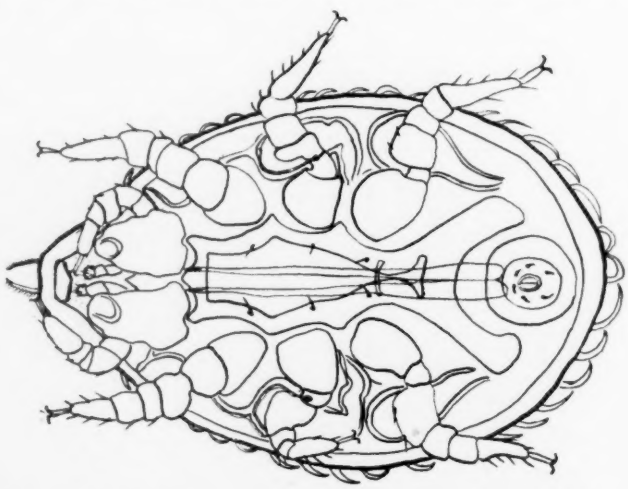


FIG. 37. *Uroobovella spinosa* n. sp. nymph: ventral view.

The chelicerae are slender, chelate, and when retracted are almost three-fifths of the length of the body; the dactyl is about one-sixteenth of the length of the basal segment. The pedipalp is slender and 5-segmented. The legs

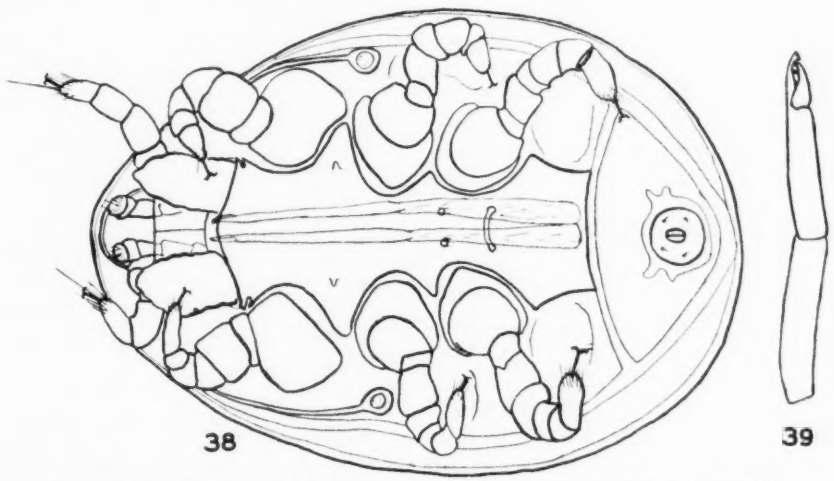
are all shorter than the width of the body. Each bears a pair of spines and a caruncle at its tip; all are sparsely setose. The bases of the first legs are indented on their anterior margin.

Type (U. S. Nat. Mus. No. 1178): Duke Forest, Durham, N. C., July 19, 1933; on *Passalus cornutus* Fabricius; Collector, A. S. Pearse.

This species was not as common as the others in the same genus.

Uroobovella levis n. sp.

Only nymphs have been collected. Body flat and almost elliptical in outline, slightly tapered anteriorly; length, 0.28 mm.; width, 0.22 mm. The dorsum is smooth, but there is a pair of small setae at both the anterior ends and a few very minute setae along the margins. The ventrum has a wide thickened margin, and impressed foveae for the legs; the posterior border of the camerostomal opening is somewhat convex; the triangular ventral and



FIGS. 38-39. *Uroobovella levis* n. sp., nymph: ventral view; 39, chelicera.

nearly circular anal plates are clearly defined; a pair of short spines between the second and third legs. On the dorsum there are a pair of small setae near the posterior margin. The curved female genital aperture is between the bases of the fourth pair of legs. The stigma is opposite the anterior border of the third pair of legs; a slightly curved peritreme extends forward from it along the side of the camerostome. All legs are provided with short pedicellate, setose tarsi, a pair of claws, and a caruncle; they are about as long as half of the width of the body and nearly equal in length. The chelicerae are a little more than half as long as the body when retracted; chelate, with the dactyl almost 1/15 of the length of the basal segment. The pedipalpi are slightly clavate and long enough to reach nearly to the anterior end of the body when retracted; the first segment is twice as long as the second, third, and fourth, which are subequal; the fifth segment is setose and hemispherical.

Type (U. S. Nat. Mus. No. 1176); Duke Forest, Durham, N. C.; August 18, 1933; on *Passalus cornutus* Fabricius; Collector, A. S. Pearse.

This mite was commonly found attached in the hollows beneath the head of Passalus. It occurred at all seasons and was, in individuals, most numerous of any species in the genus Uroobovella.

Suborder Oribatina
Family Hoplodermatidae

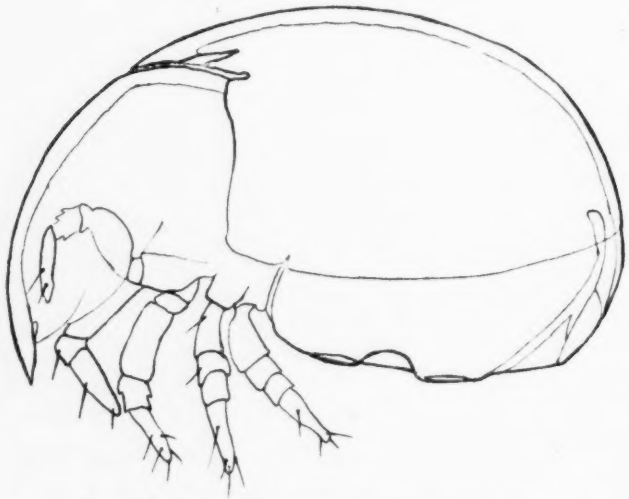


FIG. 40. Side view of hoplodermatid mite.

In June and July, 1933, a few of these peculiar mites were found on Passalus. They are readily recognized because of the cephalothorax being movably attached to the abdomen, so that the animal is able to roll up like an armadillo with the legs concealed. The specimens collected represented new genera and species. They were presented to Dr. H. E. Ewing for study.

Suborder Sarcoptina
Family Canestriniidae

Heterochelytus fusiformis Lombardini

This species was recently described (Lombardini, 1926) from passalids in Brazil. On *Passalus cornutus* in the Duke Forest it was found at all seasons beneath the elytra, and was therefore often associated with *Zercon passalorum*.

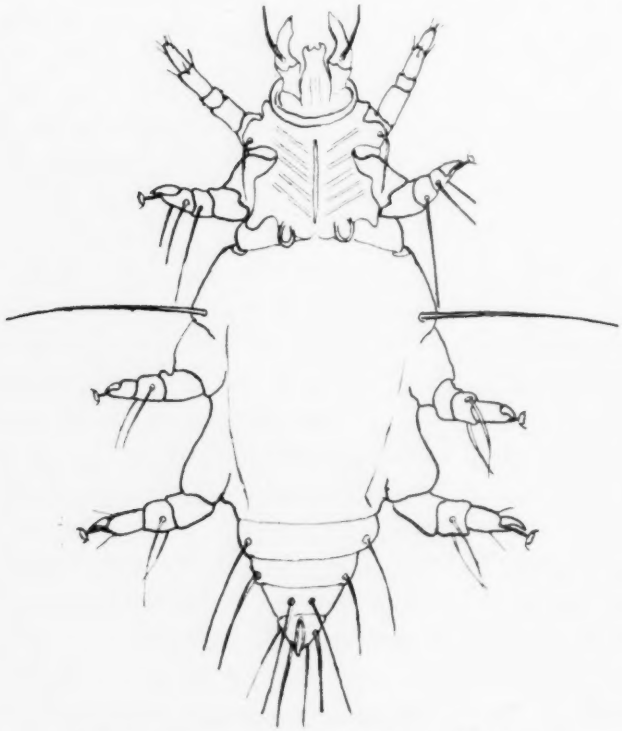
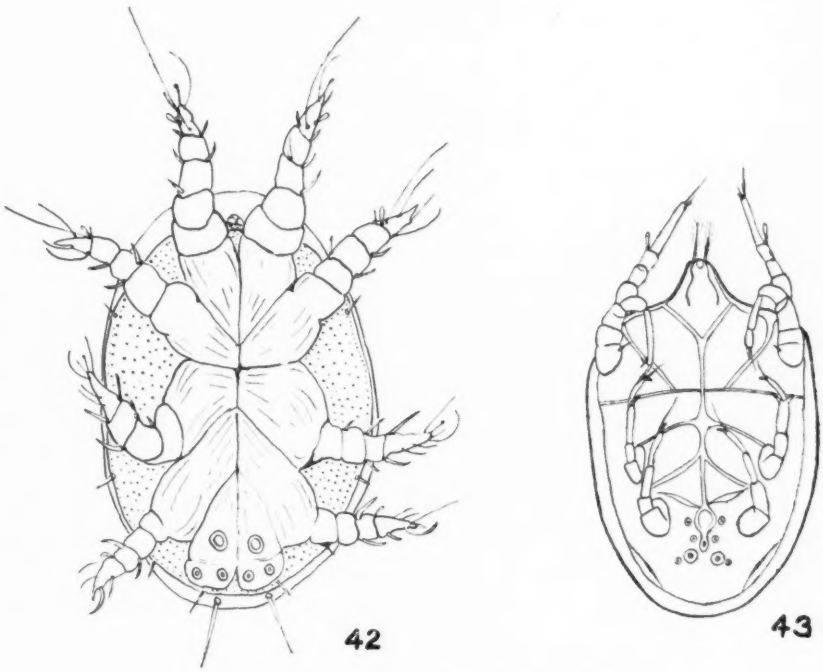


FIG. 41. Ventral view of *Heterochelytus fusiformis* Lombardini.

Family Tyroglyphidae
Hypopi

At all seasons nymphal hypopi were found on Passalus and beneath the elytra, maximum numbers occurring in the au-

tumn (Table 8). They could not be identified but two of the types are figured.



FIGS. 42-43. Ventral views of two hypopi.

Class Insectea
Superorder Dipterea
Order Dipterida
Suborder Brachycerina
Family Dexiidae
Zelia vertebrata Say

The larvae of this handsome fly were found in well grown larvae and pupae of Passalus in August and September 1933, and were very common in larvae in the autumn of 1935. Specimens were identified by Mr. David G. Hall, of the United States Bureau of Entomology.

DISCUSSION OF COMMENSALS AND PARASITES

Some of the animals associated with Passalus are probably parasites. Among these are perhaps Gregarina; the nematodes, Chondronema and Histrignathus; Heterochelytus, and the fly Zelia. Probably all the other animals are commensals; the mites: Megisthanus, Macrocheles, Caelenopsis, Passalacarus, Zercon, Uroseius, Uroobovella, hoplodermatids, hypopi.

Some of the animals which commonly live on or in Passalus show well marked seasonal distribution, others are erratic or evenly distributed throughout the year. The following list gives a general idea of conditions found by

TABLE 8. Mites on *Passalus cornutus*. Average number per month; June, 1933 to May, 1934. The first figure in each space indicates mites found on the exterior; the second, those found under the wings.

Month	January	February	March	April	May	June	July	August	September	October	November	December	Ave.
Number examined	10	10	10	10	10	10	10	10	10	10	10	10	
Magisthanus floridanus	0.5 0	0.7 0	0.2 0	0.2 0	0 0	....	....	....	0.3 0	0.3 0	0.1 0	0 0	0.26 0
Macrocheles tridentatus; Seidoes trifidus	0.2 0	4.5 0	1.6 0	2.3 0	0 0	....	....	....	2.0 0	2.7 0.1	2.0 0	0.9 0	1.80 +
Passalacarus sylvestris	2.2 0	4.1 0	0.4 0	2.3 0	2.8 0	....	....	....	5.0 0	4.6 0	6.1 0	1.5 0	3.22 0
Caelenopsis latus	1.5 0	1.7 0	0.3 0	1.2 0	0.4 0	....	....	....	1.3 0	2.4 0	2.6 0	0.8 0	1.36 0
Zercon passalorum	0 22.5	0 58.7	0 100.3	0 8.6	0.1 6.0	....	0 10.3	0 7.8	0 12.1	0 5.5	0 11.7	0 81.4	+ 29.54
Uroseius quercus	2.1 0	6.1 0	6.3 0	2.3 0	3.4 0.3	....	5.2 0.1	9.9 0	4.5 0.4	1.4 0.2	4.2 0.4	6.5 0	4.72 0.13
Uroobovella* 3 species	5.0 0	35.9 0	46.2 0	27.7 0	2.4 0	15.7 0	96.1 0	9.7 0	23.5 0	18.2 0	62.1 0.1	16.6 0	29.93 +
Heterochelytus fusiformis	0 7.7	0 6.2	0 6.0	0 2.8	0 7.7	....	0 5.6	0 2.2	0 6.8	0 0.9	0 6.1	0 8.6	0 5.51
Hypopi	2.1 0	0.4 0.9	0 0.5	0 0.4	0 0.5	....	....	2.4 0	117.2 0	2.9 0.3	15.2 0.4	1.8 40.0	14.20 4.30
Hoplodermatidae	0	0	0	0	0	0.2 0	0.9 0	0	0	0	0	0	0.09 0
Unknown	0	0	0	0	0	19.7	2.6 0	0	0	0	0	0	1.86 0
Total	13.6 30.2	53.4 65.8	55.0 106.8	36.0 11.8	9.1 14.5	35.6 0	104.8 16.0	22.0 10.0	153.8 19.3	32.5 7.0	92.3 18.7	28.1 130.0	53.02 35.84
Grand Total	43.8	119.2	161.8	47.8	23.6	35.6	120.8	32.0	173.1	39.5	111.0	158.1	88.86

* The species of Uroobovella cannot be listed separately in this table. It is almost impossible to preserve and count all the individuals present; some are destroyed and lost; but the total count is approximately correct.

the writers, each type being given in connection with the particular season when it occurs in maximum numbers:

Spring: Zercon, Macrocheles adults.

Summer: Chondronema, Macrocheles nymphs, Hoplodermidae.

Autumn: Histrignathus, Passalacarus, Caelenopsis, hypopi, Zelia.

Winter: Macrocheles and Seiodes adults, Megisthanus, Zercon.

All seasons or erratic: Gregarina, Uroseius, Uroobovella, Heterochelytus.

If the numbers of mites which occur during the colder (October-March)

and warmer (April-September) months are compared rather striking differences are apparent. For the mites which live on the outside of the body of Passalus the average number per individual is 48.8 during the cold season and 59.8 during the warm season; for those that live beneath the wings the figures are 61.4 and 12.5. The only genera of mites for which similar comparisons can be made are Uroobovella (colder season 30.8, warmer season 29.2), Zercon (colder season 50.0, warmer season 9.0), Uroseius (colder season 4.6, warmer season 5.2), and Heterochelytus (colder season 5.9, warmer season 5.0). The subelytral mite Zercon is more than ten times as abundant during the colder months, but the other mite (Heterochelytus) that lives in the same habitat shows little difference and the same is true for the two external mites.

GENERAL CONSIDERATIONS

Passalus cornutus is a beetle of large size. This is probably due to genetic constitution and has been brought about perhaps after evolution through gradual adaptation to a practically unlimited food supply and a stable habitat in rotting logs. Large animals are often vegetarians. By eating wood and the organisms associated with wood Passalus has the advantage of a food resource that is not much sought by other animals and thus avoids competition. Many insects which depend upon wood and the organisms associated with it have become specialists. Some eat wood itself, and probably represent a primitive stage in the utilization of wood as food; others eat wood with the fungi and other organisms that live in it; others raise fungus gardens on beds in which vegetation is the chief ingredient and some (attid ants) can subsist on nothing else; others eat wood and depend on protozoans, which in turn subsist on it in their enterons for food. Passalus is not very specialized in its adaptations for feeding. As an adult it can live, apparently indefinitely, on rotten wood which has been sterilized by heat to kill protozoa and fungi. Large larvae can do the same, but those just hatched apparently require something more. The young larvae will live for a few days when fed on hard, sterilized rotten wood but flourish better if the wood is finely divided and still better if it has been chewed and partially digested or converted into frass by adult beetles. Passalus is on the road to specialization in its feeding adaptations, but it has not gone far. It prefers logs of certain types of trees and rarely or never lives in others; it eats wood and relishes intermixed fungi, but can get along pretty well without the latter; it has no dependence on wood-digesting protozoans.

Large animals are more often sought by commensals, parasites, and symbionts than small. Perhaps the large size of Passalus has been responsible in part for the numerous and varied animals which have become regularly or accidentally associated with it. The fact that Passalus is colonial and has a

home which permits a certain degree of time-binding has doubtless contributed. The comparative stability of its environment has also been a factor. Passalus, among insects, is a large, slow, stupid, vegetarian, which can always be found in the same sort of a place and continues there for long periods of time. Small wonder that sixteen or more small animals have become associated with it. It may be profitable to consider briefly how and why such associations have come about.

There is not general agreement among biologists as to what a parasite, a commensal, or a symbiont is, but everyone will agree that all these are usually small plants or animals which are more or less regularly associated with one or more types of larger plants or animals (hosts) from which they receive some degree of benefit. They may show more or less adaptation to particular hosts; a dog flea or a castor bean tick may feed from many types of mammals, but a Texas fever tick will usually suck blood from nothing but cattle and a beef tapeworm will live in no definitive host but man. Often parasites do some degree of injury and take food from their hosts; commensals are innocuous guests; symbionts benefit their hosts in return for favors received. But there are many vague, confusing associations and exceptions. *Entamoeba histolytica* Schaudinn is a proper parasite of man which produces ulcers in the wall of the intestine and may cause dysentery and death. There is no doubt that it takes food, because it may be seen to engulf red blood corpuscles, and it certainly does injury. But some human hosts carry this amoeba for years without any apparent ill effects. In these this parasite is apparently a harmless commensal.

In Passalus *Chondronema passali* (Leidy) is doubtless a parasite and it is so called by Christie and Chitwood (1931) in their fine paper which describes the habits, anatomy, and life history of this nematode; yet it cannot be very injurious, for a Passalus may support thousands in its body cavity and remain strong. Beetles from which the wings have been removed under the binocular microscope show a continuous mass of wriggling nematodes through the transparent nota; yet appear to be vigorous. It is possible that some of the mites associated with Passalus may help their host by eating fungi or by some other beneficial act, perhaps some may be injurious, but at present such relations are unknown. What the present writers have demonstrated is that at least fifteen species of animals are commonly found with this beetle. Why have these particular animals associated with this particular host? The associates are not accidental; they belong to the beetles. Trombiculid mites are common in suitable places in the Duke Forest. They continually crawl over the ground and fallen logs; yet among thousands of mites no trombiculid was found on a Passalus.

It is possible that many species of mites seek logs and beetles for stability. A decaying log habitat is a guarantee against extreme changes in temperature

and desiccation. A beetle because it is a living animal, has a greater degree of stability; it has various regulating mechanisms to keep its body system operating in a steady state. Such a view of association perhaps is supported by the fact that there are ten times as many Zercons under the wings of Passalus in winter as in summer. Another sub-elytral mite, Heterochelytus, occurs in about equal numbers the year round; but this feeble, slow mite is apparently primarily adapted to live under beetles wings and nowhere else; it belongs to a group (Canestriniidae) in which mites are "of very small size and parasitic on insects" (Banks, 1915). On the other hand a Zercon is a rather speedy runner and may easily migrate from a beetle to the wood in a burrow and back again. Another difference between Zercon and Heterochelytus is that the former probably breeds outside its host, as larvae have not been found on Passalus; whereas those of the latter are often present. On February 17, 1934, masses of frass from three separate Passalus mines were examined for mites. A total of 44 cc. was carefully teased apart and searched with a binocular microscope. The result was 2 Megisthanus, 3 Macrocheles, 2 Zercon, 1 snail, and 1 crane-fly larva. Ewing (1912, 1929) says:

> The reasons for the frequent occurrence of parasitism in the Acarina are to be found largely in the minute size, the great abundance, the wide distribution and the diversity of habits of the free living members. Parasitism in a nascent state is seen today in certain living species, as for example *Pediculoides ventricosus*. A single individual of this species may be either predaceous, parasitic, or act as a scavenger. It may be either one of these or all three with equal adaptability depending entirely upon the hazards of its environment.

Most of the mites which live on the outside of the body of Passalus are probably not parasites, but commensals; the essentially sessile uropodids and hypopi get transportation, warmth, and protection. The subelytral mites are probably both parasitic. Zercon imbeds its mouth parts in the soft parts of its host; Heterochelytus has piercing and sucking mouth parts and is a typical sarcoptid.

Nematodes commonly live in decaying organic materials, including logs. Steiner (1932) has discussed the nematodes associated with beetles and says:

> From a mere occurrence of the nemas in mines of the bark beetles and their possibly accidental use of the beetles as carriers, the way to true parasitism seems to proceed by the following steps: (1) The use of the bark beetle as an unconditional carrier, (2) the extension of the carrier association into a regular life association under the wing covers or on the exterior surface of the beetle, (3) the production of special cocoons and webs by the nemas on the body of the beetle, (4) the habit of feeding on the beetle itself from the outside (ectoparasitism), and (5) true endoparasitism of nemic larvae.

Of the two nematodes in *Passalus cornutus*, Chondronema is parasitic in the body cavity during its larval development and the adults and eggs are to

be found in rotting wood; Histrignathus lives as an adult in the enteron at the anterior end of the midgut and its eggs are passed out through the anus to develop in rotting wood. Both these are obligate parasites and belong to a group of nematodes which is wholly or largely parasitic. The gregarine which is often attached to the wall of the midgut of Passalus is of course a member of the group Sporozoea, which contains nothing but parasites.

There are several questions which are raised by the study of Passalus which relate to habitat selection as related to parasitism. *Passalus cornutus* prefers oak logs as a habitat. It will be of interest to discover what types of animals are to be found in the logs of different species of trees and what types and species of parasitic animals are associated with insects in logs of various types; i.e. whether various small animals show habitat specificity for particular types of logs and whether the small animals that become associated with animal hosts show the influence of their original log habitat.

SUMMARY

1. The ecology of the beetle, *Passalus cornutus* Fabricius, has been investigated in rotting logs in the Duke Forest.

2. This beetle is colonial, a pair of parents living with a brood of their offspring. Both adults and larvae stridulate, and members of a colony are thus kept together.

3. The food of Passalus consists of rotten wood with its contained organisms. Oak is preferred, but beetles excavate mines in hickory, gum, sourwood, and sometimes even in pine, but will not work in cedar.

4. Adult beetles and well grown larvae will live for weeks in sterilized rotten wood in which all organisms have been killed by heat; but newly hatched larvae, thorgh they will live and grow for a time, will not come to maturity if fed no other food.

5. An adult beetle at 20° C. consumes 0.5 gram of wood per gram of body weight per day.

6. At least sixteen species of animals are found on or in the body of Passalus. These include a gregarine, two nematodes, twelve mites, and a fly. Two of the mites and all the other types of animals are parasites; some of the mites are merely attached to Passalus in order to obtain transportation, protection, and warmth; the relations of others are uncertain.

7. The average number of parasites and commensals found on and within a single Passalus at any time of the year is about 561: protozoans, 1.7; nematodes, 471-6; mites, 88.66; flies, 0.1.

8. Some of the animals associated with Passalus show striking seasonal variations in numbers, in some instances associated with progressive changes in the life history of the host; others are erratic or present more or less uniformly throughout the year.

9. Passalus probably attracts numerous animals because it is large, lives in a rather stable environment to which small animals resort to avoid extreme variations, and because its body furnishes a certain degree of environmental stability for commensals and parasites.

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PARASITES OF CERTAIN NORTH CAROLINA SALIENTIA

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PARASITES OF CERTAIN NORTH CAROLINA SALIENTIA

INTRODUCTION

Salientians are often infested with numerous parasites. They, therefore, provide valuable material for the study of the problems of parasitism. The variety of environmental conditions in which amphibians live gives excellent opportunities to study the relationships between parasites and environmental factors. It is remarkable that, although frogs and toads have long been used as material for the study of parasites, there has been no systematic and comprehensive study of the relations of parasitic infestations to the ages, habitats, and habits of hosts. The present paper describes attempts to make such studies on the salientians of North Carolina.

Thanks are due to Dr. A. S. Pearse, under whose direction this study was made and whose patient and helpful criticism rendered its completion possible. Drs. H. E. Ewing and J. Percy Moore identified mites and leeches, respectively. Aid in the study of helminths was given by Drs. G. Steiner, H. A. Baylis, E. W. Price and B. G. Chitwood; and in that of protozoans by Drs. R. R. Kudo and D. L. Hopkins. Dr. L. Stejneger elucidated some difficult questions of host synonymy. Drs. Allen McIntosh, R. Harkema and J. S. Rankin have been of assistance on many occasions. The writer is especially indebted to Mr. George Ross and Miss Mary Shelburne for their untiring efforts in the collection of hosts.

Previous Work

The study of North American salientians began with the work of Joseph Leidy in 1851. Before him certain European parasitologists had observed various parasites. Leeuwenhoek (Kudo, 1931) had seen Opalina and Nyctotherus. Other observers of salientian parasites included Goeze (1782), Loschge (1785), Schrank (1788), Zeder (1800), Rudolphi (1801), Creplin (1825), Mehlis (1831), Diesing (1835), and Dujardin (1845). Somewhat later van Beneden (1858), Leuckart (1865), von Linstow (1878) and Looss (1894) made important contributions.

In North America much has been done since Leidy's time. Among many works the following are among the more important. An opalinid was observed in a spadefoot by Stokes (1884). A myxosporidian, *Leptotheca ohlmacheri* (Gurley, 1893), was named in honor of its discoverer, Ohlmacher (1883). Trypanosomes and haemosporidians were found in frogs of the genus Rana and observations were made on the life-histories of the latter (Stebbins, 1904, 1905, 1907). *Nyctotherus parvus* by Walker (1909) and *Entamoeba ranarum* by Craig (1913) were reported from the same host

genus. In 1914 Metcalf began his work on Opalinidae with a description of *Zellerielia antilliensis* and went on to write a monograph (1923) in which he described many new genera, species and forms. *Trichomonas augusta, Hexamitus batrachorum* and *H. ovatus* were studied in the frogs of the western United States (Kofoid and Swezy, 1915; Swezy, 1915, 1916). Hegner (1920, 1921, 1932) recorded blood protozoans and opalinids. The life-history of *Leptotheca ohlmacheri* was studied and *Entamoeba ranarum*, Haemogregarina, *Trypanosoma rotatorium, T. parvum* and Opalina were reported by Kudo (1922). Fortner (1923) studied the frog parasites of the Douglas Lake region reporting Octomitus, Opalina and Nyctotherus. A Trichodina from a toad was described by Fulton (1923). Wenrich (1924, 1932) described an Amphileptus from the gills of tadpoles and reported Retortomonas. Beltran (1925) described an Opalina from a Mexican Hyla. Becker (1925) reported Mastigina from tadpoles. Drbohlav (1925) made observations on the occurrence of Herpetomonas, Leishmania and Trypanosoma in frogs. Tanabe (1925) reported *Karotomorpha bufonis*. Marx (1927) described *Trigonomonas diplostomum*. Sanders (1928) found Karyolysus and Lankesterella in frogs of the genus Rana. Travis (1934) reported Karotomorpha from *Rana pipiens*.

The knowledge of the trematode fauna of North American Salientia has likewise developed tremendously since the work of Leidy. Stiles and Hassall (1894) catalogued the known species. Bensley (1897) recognized two varieties of the so-called *Distomum cygnoides*. Pratt (1900, 1904) presented lists of thirteen and eighteen species respectively. Stafford, in a series of papers from 1900 to 1905, differentiated American trematodes previously confused with those of Europe and described others which were new. Seeley (1906) described *Ostiolum complexus*. Cary (1909) contributed observations on the life-history of *Diplodiscus temperatus*. Cort, in a series of papers from 1912 to 1919, added new species and other information concerning trematodes. Faust (1917) described a larval holostome from frogs. Stunkard (1917) monographed the polystomes and amphistomes. Ward (1918) gave a summary of trematodes from fresh-water hosts. Guberlet (1920) described *Gorgodera circava*. Fortner (1923) reported five species of flukes from the frogs of the Douglas Lake region. Millzner (1924a) described *Megalodiscus ranophilus*. Beaver (1929) reported *Allassostoma parvum* from frogs and determined the life-history of the trematode. Hughes (1929) reported *Diplostomulum vergrandis* from *Rana pipiens*. Irwin (1929) described *Haematolocchus parviplexus*. Hunter (1930, 1932) described *Diplodiscus intermedius* and reported Clinostomum. Miller (1930) gave a careful redescription of *Glypthelmins quieta* and synonymized Margeana with Glypthelmins. Lucker (1931) described *Haplometrana intestinalis*. Harwood (1932) described numerous species of trematodes from the Salientia of Texas.

Ingles (1932, 1932a) described *Cephalogonimus brevicirrus* and several lung flukes. Krull (1930 to 1935) made important contributions, especially in the field of life-histories. Ingles and Langston (1933) described *Gorgoderina multilobata.* Sokoloff and Caballero (1933) and Caballero and Sokoloff (1934) reported the trematode parasites of *Rana montezumae.* Stunkard and Dunihue (1933) reported Leichriorchis. Trowbridge and Hefley (1934) reported several trematodes from Oklahoma Salientia.

Since Leidy reported his *Taenia pulchella,* few cestodes have been observed in North American frogs and toads. Stiles and Hassall (1912) gave a host list for *Taenia dispar* which included *Bufo americanus, B. lentigenosus* and *Rana pipiens.* Jewell (1916) described *Cylindrotaenia americana,* as new genus and species, from *Acris gryllus, Rana pipiens* and *Bufo lentigenosus.* Dickey (1921) described *Distoichometra bufonis,* new genus and species, from *Bufo lentigenosus.* Fortner (1923) reported proteocephalids in *Rana pipiens* and *R. clamitans.* Hannum (1925) described *Ophiotaenia magna* from *Rana catesbeiana.* Osler (1931) described *Ophiotaenia saphena* from *Rana clamitans* and Thomas (1931, 1934) found that infestation resulted from the ingestion of copepods harboring the larval parasites. Harwood (1932) reported *Ophiotaenia magna* from *Rana catesbeiana* and *R. clamitans* and suggested its possible synonymy with *O. filaroides.* The same author reported *Cylindrotaenia americana* from *Acris gryllus, Hyla squirella* and *Pseudacris triseriata.* Trowbridge and Hefley (1934) reported *Ophiotaenia magna* from Bufo, Acris and Rana and *Cylindrotaenia americana* from Acris.

Five nematodes of salientians were catalogued by Stiles and Hassall (1894, 1905). Steiner (1924) described *Oswaldocruzia leidyi* along with several others from *Hyla cinerea.* Walton, in a series of papers from 1927 to 1935, has been most active in increasing the known species of salientian nematodes. Holl (1928) described *Cosmocercoides dukae* which is now known from many hosts. Canavan (1929) described the dioctophymoid, *Eustrongylides wenrichi,* from the bullfrog. Harwood (1930, 1932) has made important contributions. Travassos (1930) discussed the validity of North American species of Rhabdias. Trowbridge and Hefley (1934) reported numerous nematodes from Oklahoma Salientia.

Acanthocephala are rarely referred to in the literature relating to North American salientian parasites. Millzner (1924) described the larval *Centrorhynchus californicus* from *Hyla regilla.* Sandground (1926) has reported *Moniliformis moniliformis* from *Bufo marinus* in Honduras.

Leeches, as temporary parasites of frogs, have been reported by Nachtrieb, Hemingway and Moore (1912) and by Moore (1918).

Lernaea, a parasitic genus of Crustacea, has been found on frogs by Stunkard and Cable (1931). Shannon (1915) observed a mosquito, *Culex territans,* feeding on frogs. Darling (1910) reported the tick, *Amblyomma*

varium from *Bufo marinus* in Panama. Hooker, Bishopp and Wood (1912) reported *A. dissimile* from Bufo in Texas, Mexico, Jamaica and Panama and *A. cajennense* in a Texas Bufo. Ewing (1925) described *Hannemania hylae* from *Hyla arenicolor* and (1931) *H. penetrans* from Rana. Hubert (1927) reported a mite from *Rana sphenocephala* in Louisiana.

Relatively little work on the ecology of salientian parasites has been published. Ward (1909) reported that his student, Duncanson, had found fewest parasites in *Rana pipiens* just after spawning and that there was an increase through the following months to a maximum at hibernation. Cary (1909) studied the life-cycle of *Diplodiscus temperatus* and found that the cercariae encysted on stones and water-plants and were then ingested by tadpoles. Metcalf, in his monograph (1923) and in subsequent briefer papers, studied the opalinid parasites and advanced opinions concerning the origin and distribution of the families of Salientia. Noble (1925) has disagreed with Metcalf's conclusions. Fortner (1923), in a study of frog parasites in the Douglas Lake region of Michigan, found a variation in the parasites of frogs from different habitats. Trypanosomes were found by Hegner (1929) to occur in aquatic but not in terrestrial newts. These flagellates in Europe are transmitted by a leech (Franca, 1908). Noller (1913) reported a similar vector for Lankesterella in the same region. In America, Miss Sanders (1928) believes that Karyolysus is not transmitted by a leech but by a vector which attacks frogs only after metamorphosis.

Krull, in a series of papers from 1930 to 1934, found that frogs acquired certain lung flukes by ingesting Odonata infested with metacercariae and that they annually lost and renewed their infestations. The same author (1935) worked out the life-history of *Halipegus occidualis*. Krull and Price (1932) found that frogs became infested with *Diplodiscus temperatus* by swallowing their molted skins, on which the metacercariae had encysted. Frogs were found to serve as intermediate hosts for *Zeugorchis syntomentera* and *Alaria mustelae* by Ingles (1933a) and Bosma (1934), respectively. Ingles (1933) studied the life-history of *Ostiolum oxyorchis* and was able to synonymize *O. confusus* with it. The infestation of frogs with *Ophiotaenia saphena* by ingesting infested copepods was discovered by Thomas (1931, 1934). Joyeux (1924) states that *Cylindrotaenia americana* is capable of direct development in a single host.

Walton (1929) found that the larvae of *Rhabdias ranae* may reach the infective stage before being voided from the rectum of the host. The first larval stage of *Cosmocercoides dukae* was found to be free living and the second larval stage to be infective (Harwood, 1930). Working on the salamanders of Japan, Pearse (1932) found a significant seasonal variation in certain parasites. Trematodes and acanthocephalans were found only in acquatic hosts. Holl (1932) reported seasonal variations in parasites of Triturus and Acris and that habitat influenced the parasitic fauna.

LOCALITY STUDIED

Beaufort County, where all the writer's collecting was done, is in the east central part of North Carolina. It is located on the low-lying marine terraces of the Atlantic Coastal Plain and is generally level, with gently rolling areas near many of the streams, especially in the western end of the county. A benchmark on the courthouse at Washington, the county seat, records an altitude of about six feet above sea level. The drainage of the county varies with the topography, is generally poor, and is through the Pamlico and Pungo rivers and their tributaries. The soils consist chiefly of sands, sandy loams, muck and peat.

The climate of Beaufort County is mild. The mean annual temperature is 16.7° C. Killing frosts seldom occur after the first week in April or before the last of October. The mean annual rainfall of 145 cm. is well distributed throughout the year. The winters are generally mild, the average temperature for December, January and February being 7.4° C. The summer months, June, July and August, have an average temperature of 25.8° C. (Cobb, Vanatta, Brinkley, and McDowell, 1919).

METHODS OF INVESTIGATION

The hosts were collected by hand, usually at night with the aid of an electric flash-light. Hibernating individuals were obtained by digging in favorable places for terrestrial species and by probing under submerged ledges for those with aquatic habits. Species active in winter could best be procured on warm rainy nights along highways. Since all the salientians studied were taken in Beaufort County and examinations were made at Duke University, a delay of from one to several days between collections and examinations was unavoidable. On this account, data regarding food habits are meagre. The animals were examined for parasites externally and internally under a binocular microscope. The parasites were removed, counted and either studied alive or prepared for permanent mounts.

Smears of intestinal contents, blood, kidneys and other organs were examined under the compound microscope for smaller protozoan parasites. Permanent preparations of blood protozoans were made by fixating with 95 per cent alcohol and treating with Giemsa's stain. Other protozoans were fixed in Schaudinn's fluid and stained with iron-hematoxylin and occasionally counterstained with eosin.

Trematodes were washed in normal saline, relaxed in tap water, fixed with Conant's fluid or Bouin's fluid, stained with Grenacher's borax-carmine, Ehrlich's hematoxylin or cochineal, and mounted in damar. Some of the worms were serially sectioned but most of them were preserved as toto mounts. Sections were stained with Ehrlich's hematoxylin using eosin as a counterstain.

Cestodes were treated in the same manner as trematodes. Some of the cylindrical worms were pressed flat between glass plates before fixation in order to facilitate study of toto mounts. Serial sections were also prepared.

Nematodes were washed in normal saline then either relaxed in tap water or fixed at once in 70 per cent alcohol. The worms were stored in the latter fluid and mounted for study in glycerine, lacto-phenol or creosote.

Acanthocephalans were treated in the same manner as trematodes.

Leeches were preserved in 10 per cent formalin.

Mites were fixed in Conant's fluid or were mounted directly in Berlese's medium (Lee, 1928, p. 514).

HOSTS EXAMINED

Twenty-six species of Salientia are known to occur in North Carolina. Of these twenty-two have been found in Beaufort County. After four months of preliminary examinations, six species were selected for study through a complete annual cycle. These had been found in an earlier study (Brandt, 1936) to be available at all seasons of the year. In respect to habitats they may be classified into a series as aquatic, semi-aquatic, palustrine, terrestrial, fossorial and arboreal species. The original plan involved the examination of five individuals of each host species in each month of the year and this schedule was adhered to as closely as possible. All of the animals used were taken in Beaufort County.

Aquatic Species: *Rana catesbeiana* Shaw 1802

The bullfrog is the most completely aquatic species of the region. Its range includes "North America east of the Rocky Mountains except the extreme southeast and Gulf states coastal plain" (Stejneger and Barbour, 1933). In North Carolina, Brimley (1926) gives the range as statewide. The species is active to some extent in every month of the year but most large individuals hibernate. By dint of careful search it was possible to procure fourteen hibernating individuals of large size for the winter examinations. Only very small individuals were observed to be active during the winter of 1934-35. In Beaufort County the species has been observed to breed in April and May. Because there was a considerable difference in the number of parasites found in large and in small bullfrogs, it seemed desirable to separate the group into two series, large and small. The length, 100 mm., represents the minimum breeding size (Wright, 1931), and was therefore selected as the point of division. The lengths of the thirty-three large bullfrogs examined average 142.3 mm. The extreme lengths were 100.0 mm. and 175.0 mm. The thirty-eight small bullfrogs average 44.9 mm. in length. The extreme lengths were 32.6 mm. and 82.5 mm. The entire series of seventy-one bullfrogs averaged 90.1 mm. in length. Since the bullfrog is never very numerous in a single restricted locality, it was necessary to take hosts from numerous localities. The con-

tents of the enterons of the hosts consisted of crayfish (27.7%), sand (19.7%), insects (17.8%), molted skins (16.0%), debris (9.8%), snails (5.3%), and small frogs (3.7%). The seasonal distribution of hosts is shown in Table 1.

Semi-aquatic Species: *Rana sphenocephala* (Cope, 1886)

The southern leopard-frog is distinctly less aquatic than the cogeneric bullfrog, but it spends much time in and near the water. Stejneger and Barbour (1933) give "southeastern states" as the range of the species. Brimley (1926) gives the range in North Carolina as "eastern district." This includes all of the coastal plain and portions of the Piedmont region. The great abundance of the species permitted the procuring of five mature individuals each month from a certain small pond. The lengths of these animals averaged 55.1 mm. The extremes measured 40.6 mm. and 73.6 mm. in length. The enterons of the hosts contained molted skins (59.0%), debris (16.7%), insects (8.9%), spiders (5.9%), earthworms (.83%), and myriapods (.40%). The seasonal distribution of hosts is shown in Table 1.

Terrestrial Species: *Bufo fowleri* Hinckley 1882

Fowler's toad is characteristically terrestrial. However, it visits an aquatic environment for about two months of the year when breeding. The range is "New England and New York, southward to Georgia, west to Michigan and Missouri, but occurring also on the Atlantic and Gulf coastal plain to central Texas. (Not known in peninsular Florida)" (Stejneger and Barbour, 1933). The range in North Carolina is statewide (Brimley, 1926). During the winter it was necessary to dig out individuals hibernating under heaps of litter. The sixty-two hosts examined averaged 48.5 mm. in length. The extreme lengths were 30.9 mm. and 64.0 mm. The enterons of the animals examined contained sand (36.3%), molted skins (30.6%), debris (22.8%), and insects (10.3%). The seasonal distribution of hosts is shown in Table 1.

Fossorial Species: *Scaphiopus holbrookii* (Harlan, 1835)

The spadefoot is more distinctly terrestrial than Fowler's toad. The time spent in an aquatic environment when breeding is always limited and has been stated to be restricted in some years to a single day Hibernating animals were dug from a depth of about six inches in well drained, sandy areas. The range of the spadefoot includes "eastern states, Massachusetts to Florida, west to Louisiana, Texas to Arkansas" (Stejneger and Barbour, 1933). The range in North Carolina includes Wake, Carteret, Henderson, Beaufort, Pitt, Greene, Wilson, Nash and Columbus counties (Brandt, 1936). The average length of the individuals examined was 51.0 mm. The extremes in length were 23.5 mm. and 67.0 mm. The enterons of the hosts examined contained

insects (41.4%), sand (36.4%), debris (12.3%), myriapods (5.9%), snails (3.0%), spiders (0.6%), and seeds (0.4%). The seasonal distribution of hosts is shown in Table 1.

Palustrine Species: *Pseudacris brimleyi* Brandt and Walker 1933

This chorus frog was selected as the representative of an arboreal form which has reverted to terrestrial life. It is of especial interest in comparison with its more arboreal relative of similar size, *Hyla crucifer*. About four months are spent at the breeding pools; the remainder of the year this species usually spends along swampy shores. The known range (Brandt and Walker, 1933) includes "southern Virginia to Northern Georgia, along the coast" In North Carolina it is known from Beaufort, Pitt, Greene, Craven, Edgecombe and Wilson counties (Brandt, 1936). The fifty-five hosts averaged 27.4 mm. in length. The extreme lengths were 19.9 mm. and 34.3 mm. The enterons of the animals contained insects (75.0%), spiders (16.7%), and debris (8.3%). The seasonal distribution of hosts is shown in Table 1.

Arboreal Species: *Hyla crucifer* Wied 1838

The spring-peeper is the most arboreal of the species in the series studied. About four months exposure to an aquatic environment occurs at the breeding season. The range of *Hyla crucifer* includes "New Brunswick to Manitoba, south to Georgia, Louisiana, Arkansas and Kansas" (Stejneger and Barbour, 1933). In North Carolina, the range is statewide (Brimley, 1926). The sixty hosts examined averaged 26.4 mm. in length. The extremes in length were 14.9 mm. and 33.0 mm. The enterons contained insects (57.6%), debris (20.6%), molted skins (16.6%) and sand (5.2%). The seasonal distribution of hosts is shown in Table 1.

PARASITES OF HOSTS EXAMINED

In the following section is given a list of parasites found in the six species of hosts during the annual cycle from March, 1934 to March, 1935. Following the name of each parasite there may be one or two numbers. The first indicates the percentage infestation and the second, when present, indicates the average number of parasites per host. Finally, the part of the host's body infested is given.

Rana catesbeiana (OVER 100 MM. LONG)

The thirty-three large bullfrogs examined contained the following parasites:

Protozoa

Cytamoeba bactifera Labbe 1894; 6.06%; erythrocytes
Entamoeba ranarum Grassi 1879; 3.03%; intestine
Unidentified cysts; 42.4%; muscles

Karyolysus sp. or *Lankesterella* sp.; 24.2% ; blood
Leptotheca ohlmacheri (Gurley 1893) ; 3.03% ; kidney
Nyctotherus cordiformis (Ehrenberg 1838) ; 9.1% ; intestine
Octomitus intestinalis Prowazek 1904; 84.8% ; intestine
Trichomonas augusta Alexeieff 1911; 97.0% ; intestine
Trypanosoma rotatorium (Mayer 1843) ; 9.1% ; blood

Trematoda

Diplodiscus temperatus Stafford 1905; 24.3% ; 0.85% ; rectum
D. intermedius Hunter 1930; 54.6% ; 6.2; rectum
All *Diplodiscus;* 72.8% ; 7.3; rectum
Glypthelmins subtropica Harwood 1932; 54.6% ; 4.03; intestine
Gorgodera amplicava Looss 1899; 63.8% ; 8.4; urinary bladder
Gorgoderina attenuata (Stafford 1902) ; 9.1% ; 1.64; kidney and bladder
All *Gorgoderinae;* 69.7% ; 10.0; kidney and urinary bladder
Haematoloechus sp.; 18.2% ; 0.27; lungs
H. breviplexus Stafford 1902; 33.3% ; 1.67; lungs
H. longiplexus Stafford 1903; 9.1% ; 0.15; lungs
Loxogenes bicolor Krull 1933; 36.4% ; 1.49; pancreas and liver
Encysted flukes; 75.7% ; 22.8; general

Cestoda

Ophiotaenia saphena Osler 1931; 9.1% ; 0.091; intestine
Proteocephalid cysts; 42.4% ; 32.5; general

Nematoda

Agamascaris odontocephala Steiner 1924; 42.4% ; .697; body cavity
Agamonema cysts; 90.9% ; 127.2; general
Cosmocercoides dukae (Holl 1928) ; 12.1% ; 1.24; intestine
Dujardinia sp.; 21.2% ; 0.76; body cavity
Foleyella americana Walton 1929; 3.03% ; 0.06; body cavity
F. ranae Walton 1929; 51.6% ; 3.64; body cavity
Microfilaria sp.; 30.3% ; blood
Oswaldocruzia pipiens Walton 1929; 9.1% ; 0.121; intestine
Oxysomatium longicaudata (Walton 1929) ; 24.3% ; 6.22; enteron
Physaloptera sp.; 42.4% ; 1.69; stomach
Rhabdias sp.; 3.03% ; 0.06; body cavity
R. ranae Walton 1929; 12.1% ; 0.18; lungs
Spironoura catesbeianae (Walton 1929) ; 45.5% ; 28.0; intestine
Spiroxys sp.; 9.1% ; 0.70; enteron

Acanthocephala

Centrorhynchus sp.; 81.8% ; 13.9; body cavity

Hirudinea

Macrobdella ditetra Moore undescribed; 12.1%; 0.303; external

Acarina

Hannemania penetrans Ewing 1931; 12.1%; 0.243; skin

Rana catesbeiana (UNDER 100 MM. LONG)

The thirty-eight small bullfrogs examined contained the following parasites:

Protozoa

Entamoeba ranarum Grassi 1879; 13.2%; intestine
Karyolysus sp. or *Lankesterella* sp.; 5.25%; blood
Leptotheca ohlmacheri (Gurley 1893); 34.2%; kidney
Octomitus intestinalis Prowazek 1904; 97.4%; intestine
Trichomonas augusta Alexeieff 1911; 73.7%; intestine
Trypanosoma rotatorium (Mayer 1843); 10.5%; blood
Unidentified flagellate; 10.5%; intestine

Trematoda

Diplodiscus temperatus Stafford 1905; 36.8%; 1.53; rectum
D. intermedius Hunter 1930; 7.91%; 0.263; rectum
All *Diplodiscus;* 47.3%; 1.84; rectum
Glypthelmins subtropica Harwood 1932; 2.63%; 0.395; intestine
Gorgodera amplicava Looss 1899; 2.63%; 0.0263; urinary bladder
Gorgoderina attenuata (Stafford 1902); 5.25%; 0.132; urinary bladder
All bladder flukes; 7.9%; 0.158; urinary bladder
Haematoloechus breviplexus Stafford 1902; 10.5%; 0.105; lungs
H. longiplexus Stafford 1902; 5.25%; 0.0525; lungs
All *Haematoloechus;* 18.4%; 0.42; lungs
Loxogenes bicolor Krull 1933; 44.7%; 0.947; pancrea and liver
Larval flukes; 63.2%; 6.72; general

Cestoda

Proteocephalid cysts; 42.2%; 3.58; general

Nematoda

Agamascaris odontocephala Steiner 1924; 2.63%; 0.0263; body cavity
Agamonema sp.; 18.4%; 0.474; general
Cosmocercoides dukae (Holl 1928); 2.63%; 0.0263; intestine
Foleyella americana Walton 1929; 2.63%; 0.0263; body cavity
Oswaldocruzia pipiens Walton 1929; 18.4%; 0.342; intestine
Spironoura catesbeianae (Walton 1929); 2.63%; 0.0263; intestine
Rhabdias sp.; 21.1%; 0.474; body cavity
R. ranae Walton 1929; 15.8%; 0.237; lungs

Acanthocephala

Centrorhynchus sp.; 5.25% ; 0.132; body cavity

Hirudinea

Macrobdella ditetra Moore undescribed; 5.25% ; 0.079; external

Rana sphenocephala

The sixty *Rana sphenocephala* examined were infested with the following parasites:

Protozoa

Cytamoeba bacterifera Labbe 1894; 40.0% ; erythrocytes
Entamoeba ranarum Grassi 1879; 1.67% ; intestine
Karyolysus sp. or *Lankesterella* sp.; 28.3% ; blood
Leptotheca ohlmacheri (Gurley 1893); 10.0% ; kidney
Nyctotherus cordiformis (Ehrenberg 1838); 13.3% ; intestine
Octomitus intestinalis Prowazek 1904; 90.0% ; intestine
Opalina sp.; 1.67; intestine
O. carolinensis Metcalf 1923; 20.0% ; intestine
O. kennicotti Metcalf 1923; 1.67% ; intestine
O. obtrigonoidea Metcalf 1923; 15.0% ; intestine
All *Opalina;* 30.0% ; intestine
Trypanosoma rotatorium (Mayer 1843); 38.3% ; blood
Trichomonas augusta Alexeieff 1911; 78.4% ; intestine
Unidentified flagellate; 10.0% ; intestine

Trematoda

Brachycoelium hospitale (Stafford 1900); 3.33% ; 0.216; intestine
Cephalogonimus americanus Stafford 1902; 1.67% ; 0.0167; intestine
Diplodiscus temperatus Stafford 1905; 40.0% ; 0.867; rectum
Gorgoderina attenuata (Stafford 1902); 5.0% ; 0.083; urinary bladder
Loxogenes bicolor Krull 1933; 5.0% ; 0.01; pancreas and liver
Ostiolum complexus (Seeley 1906); 56.7% ; 5.72; lungs
Larval flukes; 53.5% ; 37.8; general

Cestoda

Proteocephalid cysts; 51.7% ; 10.1; general

Nematoda

Agamascaris odontocephala Steiner 1924; 16.7% ; 0.467; body cavity
Agamonema sp.; 63.3% ; 4.16; general
Cosmocercoides dukae (Holl 1928); 3.33% ; 0.083; intestine
Dujardinia sp.; 5.0% ; 0.117; body cavity
Foleyella sp.; 1.67% ; 0.033; body cavity
F. americana Walton 1929; 23.7% ; 0.733; body cavity

F. ranae Walton 1929; 11.7%; 0.267; body cavity
All *Foleyella;* 35.0%; 1.033; body cavity
Microfilaria sp.; 6.67%; blood
Oswaldocruzia pipiens Walton 1929; 48.3%; 2.18 intestine
Rhabdias sp.; 58.3%; 8.78; body cavity
R. ranae Walton 1929; 48.3; 2.48; lungs

Acanthocephala

Centrorhynchus sp.; 28.3%; 2.62; body cavity

Acarina

Hannemania penetrans Ewing 1931; 6.67%; 0.10; skin

Bufo fowleri

The sixty-two *Bufo fowleri* examined contained the following parasites:

Protozoa

Nyctotherus cordiformis (Ehrenberg 1838); 35.5%; intestine
Octomitus intestinalis Prowazek 1904; 53.2%; intestine
Opalina sp.; 1.61%; intestine
O. obtrigonoidea Metcalf 1923; 20.9%; intestine
O. triangulata Metcalf 1923; 1.61%; intestine
O. virguloidea Metcalf 1923; 6.45%; intestine
Trichomonas augusta Alexeieff 1911; 93.5%; intestine
Trypanosoma rotatorium (Mayer 1843); 3.21%; blood

Trematoda

Brachycoelium hospitale (Stafford 1900); 1.61%; 0.016; intestine
Gorgodera amplicava Looss 1899; 1.61%; 0.016; urinary bladder
Gorgoderina attenuata (Stafford 1902); 3.21%; 0.065; urinary bladder
G. simplex (Stafford 1902); 1.61%; 0.016; urinary bladder
G. translucida (Stafford 1902); 1.61%; 0.032; urinary bladder
All bladder flukes; 8.07%; 0.129; urinary bladder
Larval flukes; 21.0%; 0.581; general

Cestoda

Distoichometra bufonis Dickey 1921; 40.3%; 1.97; enteron
Proteocephalid cysts; 3.21%; 1.61; general

Nematoda

Agamonema sp.; 42.5%; 15.8; general
Cosmocercoides dukae (Holl 1928); 30.7%; 0.483; intestine
Oswaldocruzia pipiens Walton 1929; 61.3%; 3.5; intestine
Physaloptera sp.; 1.61%; 0.0161; stomach
Rhabdias sp.; 1.61%; 0.032; body cavity
R. ranae Walton 1929; 1.61%; 0.0483; lungs

Acanthocephala

Centrorhynchus sp.; 1.61% ; 0.0161 ; body cavity

Acarina

Hannemania penetrans Ewing 1931 ; 4.83% ; 0.145 ; skin

Scaphiopus holbrookii

The sixty *Scaphiopus holbrookii* examined contained the following parasites:

Protozoa

Nyctotherus cordiformis (Ehrenberg 1838) ; 58.3% ; intestine
Octomitus intestinalis Prowazek 1904 ; 61.8% ; intestine
Opalina carolinensis Metcalf 1923 ; 1.67% ; intestine
O. oblanceolata Metcalf 1923 ; 10.0% ; intestine
O. obtrigonoidea Metcalf 1923 ; 10.0% ; intestine
O. triangulata Metcalf 1923 ; 6.7% ; intestine
Trichomonas augusta Alexeieff 1911 ; 76.4% ; intestine

Cestoda

Distoichometra bufonis Dickey 1921 ; 16.7% ; 0.92 ; enteron
Proteocephalid cysts ; 1.7% ; 0.33 ; intestinal wall

Nematoda

Agamonema sp. ; 26.7% ; 5.62 ; general
Cosmocercoides dukae (Holl 1928) ; 71.7% ; 10.0 ; intestine
Oswaldocruzia leidyi Travassos 1917 ; 13.3% ; 0.23 ; intestine
O. pipiens Walton 1929 ; 38.3% ; 1.52 ; intestine
Physaloptera sp. ; 3.3% ; 0.20 ; stomach
Rhabdias sp. ; 1.7% ; 0.017 ; body cavity
R. ranae Walton 1929 ; 1.7% ; 0.017 lungs

Pseudacris brimleyi

The fifty-five *Pseudacris brimleyi* examined contained the following parasites:

Protozoa

Nyctotherus cordiformis (Ehrenberg 1838) ; 30.9% ; intestine
Octomitus intestinalis Prowazek 1904 ; 56.3% ; intestine
Opalina chorophili Metcalf 1923 ; 45.5% ; intestine
O. hylaxena Metcalf 1923 ; 1.8% ; intestine
O. oblanceolata Metcalf 1923 ; 1.8% ; intestine
O. obtrigonoidea Metcalf 1923 ; 9.1% ; intestine
O. pickeringii Metcalf 1923 ; 16.4% ; intestine
O. virguloidea Metcalf 1923 ; 12.7 ; intestine

Trichomonas augusta Alexeieff 1911; 30.9%; intestine
Trypanosoma rotatorium (Mayer 1843); 1.8%; blood
Unidentified flagellate; 1.8%; intestine

Trematoda

Brachycoelium hospitale (Stafford 1900); 72.8%; 6.69; intestine
Diplodiscus temperatus Stafford 1905; 5.5%; 0.055; rectum
Larval flukes; 3.6%; 2.36; general

Nematoda

Agamascaris odontocephala Steiner 1924; 1.8%; 0.018; body cavity
Agamonema sp.; 9.1%; 0.47; general
Cosmocercoides dukae (Holl 1928); 78.2%; 2.64; intestine
Oswaldocruzia pipiens Walton 1929; 40.0%; 1.05; intestine
Physaloptera sp.; 3.6%; 0.092; stomach
Rhabdias sp.; 18.2%; 0.38; body cavity
Rhabdias ranae Walton 1929; 41.8%; 0.80; lungs

Acanthocephala

Centrorhynchus sp.; 7.3%; 0.127; body cavity

Hyla crucifer

The sixty *Hyla crucifer* examined contained the following parasites:

Protozoa

Nyctotherus cordiformis (Ehrenberg 1838); 43.3%; intestine
Octomitus intestinalis Prowazek 1904; 66.7%; intestine
Opalina sp.; 6.67%; intestine
O. chorophili Metcalf 1923; 5.0%; intestine
O. hylaxena Metcalf 1923; 5.0%; intestine
O. obtrigonoidea Metcalf 1923; 21.7%; intestine
O. pickeringii Metcalf 1923; 48.3%; intestine
O. virguloidea Metcalf 1923; 5.0%; intestine
Trichomonas augusta Alexeieff 1911; 65.0%; intestine
Trypanosoma rotatorium (Mayer 1843); blood

Trematoda

Brachycoelium hospitale (Stafford 1900); 6.67%; 0.167; intestine
Diplodiscus temperatus Stafford 1905; 3.33%; 0.033; rectum
Glypthelmins sp.; 18.3%; 1.82; intestine
Larval flukes; 3.33%; 0.033; general

Cestoda

Proteocephalid cysts; 3.33%; 0.134; general

Nematoda

Agamascaris odontocephala Steiner 1924; 1.67%; 0.0167; body cavity
Agamonema sp.; 25.0%; 7.48; general
Cosmocercoides dukae (Holl 1928); 13.4%; 0.167; intestine
Oswaldocruzia pipiens Walton 1929; 8.33%; 0.55; intestine
Physaloptera sp.; 3.33%; 0.067; stomach
Rhabdias sp.; 1.67%; 0.05; body cavity
R. ranae Walton 1929; 3.33%; 0.083; lungs

Acanthocephala

Centrorhynchus sp.; 1.67%; 0.0167; body cavity

SEASONAL VARIATION

Tables 7 to 13 present the data concerning seasonal variation of the parasites of the hosts examined. The groupings used, rather than the tabulation by months, were selected in order to increase the size of the groups thus increasing the statistical reliability of the data.

Study of these tables indicates that much of the variation shown is not particularly significant. This is true of the protozoans infesting the intestine. The blood protozoans, however, appeared to exhibit a significant seasonal variation. Trypanosomes were more common in Rana during the warmer periods of the year. They were found in *Bufo fowleri* in August, in *Hyla crucifer* from December to May, and once in *Pseudacris brimleyi* in October. The haemosporidians, Karyolysus and Lankesterella, were more common in the warmer part of the year. Cytamoeba was more prevalent in the colder part of the year.

Lung flukes were less abundant at the breeding season of *Rana catesbeiana* and *R. sphenocephala*. The large bullfrogs had most bladder flukes in the summer and fewest in February. *Rana sphenocephala* had, however, its maximum infestation in February. *Bufo fowleri* harbored most bladder flukes in late summer and autumn.

Flukes of the genus Diplodiscus were very variable in the small bullfrogs but in the large individuals the parasite is most common at hibernation and least common at the breeding season. *Rana sphenocephala* harbors few Diplodiscus in spring, many in August, and fewer thereafter. These parasites were rare or absent in other hosts.

Brachycoelium hospitale was present in *Hyla cricufer* during the breeding season and shortly thereafter. The highest infestation in *Pseudacris brimleyi* occurred at about the breeding season and the lowest occurred in midsummer. This parasite was rare in *Rana sphenocephala* and was found only in the first half of the year.

Encysted trematodes occurred in all hosts except the spadefoot. Their frequency in *Bufo fowleri* and the large *Rana catesbeiana* appeared haphazard.

In *Hyla crucifer* there was one in each February and May. They were similarly rare in *Pseudacris brimleyi*. *Rana sphenocephala* showed a less infestation at the breeding season and more during the succeeding months.

Loxogenes bicolor showed a rather constant frequency in large bullfrogs but was absent late in the period of hibernation. The occurrence of this fluke was more variable in small bullfrogs and showed a maximum in early summer. *Rana sphenocephala* harbored few of the parasites, with the greatest incidence in May.

In the large bullfrogs mature cestodes were found only during a brief period after breeding. They were found only in the large *Rana catesbeiana*, *Bufo fowleri* and *Scaphiopus holbrookii*. Proteocephalid cysts occurred in all species except *Pseudacris brimleyi*. They tended to be more frequent after the hosts had visited an aquatic environment.

Bufo fowleri contained more Oswaldocruzia in midsummer; *Scaphiopus holbrookii* had a maximum infestation in March with a gradual decrease thereafter; *Hyla crucifer* harbored more of the parasites early in the winter; and *Pseudacris brimleyi* exhibited its greatest percentage of infestation later in the winter. *Rana sphenocephala* harbored more Oswaldocruzia at the breeding season and least in midsummer. The small bullfrogs harbored more of these parasites in March, while the large bullfrogs contained them chiefly at the breeding season.

Foleyella in the large bullfrogs, showed a minimum in July and a maximum in December. The small bullfrogs had but a single infestation. *Rana sphenocephala* had fewer of the parasites at and just after breeding and more in early winter. Microfilaria were most common early during the hibernation of the large *Rana catesbeiana* and least common at the breeding season. *R. sphenocephala* also harbored them less frequently at the breeding season. The maximum infestation occurred early in winter.

Rhabdias, in the large bullfrogs, became more prevalent through the summer and early autumn. Small bullfrogs harbored more in August and least in May. *Rana sphenocephala* showed its highest infestation in February and least in May. In *Pseudacris brimleyi*, this parasite was most frequent in March and least so in August. Rhabdias was rare in the other hosts.

Cosmocercoides occurred in all species of hosts studied. The parasite appeared to be more abundant at about the time of breeding.

The larval acanthocephalan, Centrorhynchus, was more common in *Rana sphenocephala* at the breeding season. The large bullfrogs tended toward constancy in percentage of infestation but more individuals harbored the parasites during hibernation. Infestation was uncommon in the other hosts studied.

Macrobdella ditetra was found only in midsummer on bullfrogs and not on other hosts. *Hannemania penetrans* was found on the toad and on the large

bullfrogs only in summer. *Rana sphenocephala* showed a greater infestation by this mite in May and less in late summer.

DISCUSSION

The Salientia are of especial interest to a parasitologist. They possess a considerable degree of general similarity yet show a range of habitats, sizes, and habits which profoundly influence their parasitic faunas. They support a wide variety of parasites. The small size of salientians makes them comparatively easy to examine. Their recognized value has led to their extensive use as laboratory animals in the teaching of parasitology. They have not received adequate recognition as material for the investigation of the fundamental problems of the ecology of parasites. Those of North Carolina provide excellent material for the study of ecological problems related to parasitism. The eastern district of the state is inhabited by twenty-four species of frogs and toads. These live in habitats ranging from aquatic to those which are more or less completely terrestrial, fossorial, and arboreal. Parasites often occur in great variety and large numbers. The mild climate permits many species of hosts to remain active for the greater part of the winter. Opportunity is offered to make interesting comparisons of the effect of habitat on parasites, of seasonal variation, host specificity, multiple infestation, and other ecological phenomena.

The observations discussed in this section were based in part on the results of the writer's examinations of seventy-one bullfrogs, sixty southern leopard-frogs, sixty-two Fowler's toads, sixty spadefoots, fifty-five chorus-frogs, and sixty spring peepers. The hosts were taken at fairly regular intervals throughout the year from March, 1934 to March, 1935 (Table 1). The species selected are of especial interest in that each is characteristic of a different habitat.

PARASITES AND HABITATS

The species of Salientia studied by the writer can be arranged in a series comprising various extents of preference for aquatic, terrestrial, and arboreal habitats. None of the frogs and toads studied have attained complete freedom from the water. Even the most completely terrestrial, the fossorial spadefoot, must visit an equatic environment in order to spawn but may limit this visit to a single day annually. The other five species spend considerable time at the ponds and streams.

Table 2 shows that salientians at Washington, North Carolina, are almost always parasitized by protozoans, especially those that live in the intestine. Blood protozoans are more often found in the aquatic hosts. This observation agrees with the findings of Hegner (1929) who studied the protozoans in the aquatic and terrestrial phases of *Triturus viridescens* and suggests an inter-

mediary aquatic blood-sucking vector. Except for their unusual abundance in the hylids, intestinal ciliates appear to become more prevalent as more completely terrestrial host species are considered.

The most aquatic species, *Rana catesbeiana*, showed a greater infestation with metazoan parasites than did any other species Metazoan parasites (Table 14) were found in every individual of this host species except one which was very young. The average number of metazoan parasites was 133. The distinctly less aquatic southern leopard-frog contained metazoan parasites in every case but the average number was less (76.7). Fowler's toad, which spends but about one month annually in an aquatic environment, showed metazoan parasites in all cases but two. The average number of metazoan parasites was 23.9. The least aquatic species, the spadefoot, harbored metazoan parasites in 83.3 per cent of the sixty hosts examined. The average number of parasites per host was 18.9. The data from comparisons of frogs and toads of moderate size suggest a high correlation between an aquatic habitat preference and degree of metazoan parasitism.

Continuing the comparison to include the two small hylids studied, it is apparent that *Hyla crucifer* contained distinctly fewer metazoan parasites than did *Pseudacris brimleyi*. The former was infested to the extent of 65 per cent, average number per host 10.6; the latter was infested in 98.2 per cent of the individuals examined and harbored an average number of 14.7. These data suggest that an arboreal habitat is less conducive to metazoan parasitism than a more terrestrial habitat.

More trematode parasites occur in aquatic than in terrestrial species of hosts (Table 3). This finding is in agreement with those of Pearse (1932) in his study of the parasites of Japanese salamanders. The preponderance of lung flukes in the more aquatic hosts is understandable in light of the work done on the life-histories of these trematodes (Krull 1930, 1931, 1932, 1933, 1934; Ingles 1933), all of which require aquatic intermediate hosts in addition to snails. The prevalence of larval flukes is significantly correlated with residence of the host in an aquatic habitat. This correlation is in agreement with the known methods of entrance of cercariae and metacercariae both by direct penetration of the skin of the host and by ingestion with food of aquatic origin. The complete absence of flukes from the least aquatic species, the spadefoot, is noteworthy. This suggests that the assumption of a subterranean habitat with an almost complete reduction of the time spent in an aquatic habitat at the breeding season, has minimized effectively the continuance of trematode parasitism. In the Hylidae, it appears that the resumption of palustrine life, as illustrated by *Pseudacris brimleyi*, has increased the degree of trematode parasitism. *Hyla crucifer*, however, living in a less monotonous habitat than does *Pseudacris brimleyi*, contained a greater variety of parasite species.

A comparison of cestode parasites is presented in Table 4. Cestode infestation does not show the correlation with habitat so clearly indicated in the foregoing discussion. That habitat preference is an important factor is apparent but it is also clear that no single factor is sufficient in itself to explain all the observations. It is likewise apparent here that host specificity is of considerable importance especially in reference to adult cestodes. *Distoichometra bufonis* is known only from Bufo and Scaphiopus hosts. The similarity in adaptation of these hosts suggests the possibility of similarity in internal physiological conditions. The differently adjusted, more aquatic species do not harbor this common salientian cestode. It is worthy of note that the Bufo harbors significantly more of these cestodes than does Scaphiopus and this observation suggests that Distoichometra may resemble *Ophiotaenia saphena* in gaining entrance to its definitive host through ingested food of aquatic origin (Thomas 1931). The evidence presented herein does not suggest the direct development of Distoichometra, as has been found for the closely related Cylindrotaenia (Joyeux 1924).

Data concerning the variation of nematode parasites is presented in Table 5. It appears that a lower percentage of infestation by nematodes occurred in the arboreal spring-peeper than in the more terrestrial chorus-frog. This is especially noticeable in the prevalence of nematodes inhabiting lungs and intestine. Agamonema, however, was much more prevalent in the tree frog. Comparison of Scaphiopus, Bufo and Rana shows no significant regularity in nematode infestation in general. Pearse (1932) found that the nematodes of Japanese salamanders from different habitats were erratic in distribution. Considering the prevalence of encysted nematodes and nematodes of the intestine of hosts of the same three genera, the irregularity again is apparent. In the case of the filaroids, which were restricted to hosts of the genus Rana, a significant correlation appears and this suggests that these nematodes are in some manner connected with an aquatic blood-sucking vector. Rhabdias is prevalent only in the two palustrine species. This observation suggests that the free living stages of Rhabdias reach an optimum in a moist terrestrial habitat. The distribution of Oswaldocruzia suggests a similar adjustment to a considerably less moist terrestrial habitat. Intestinal oxyuroids tend to be more prevalent in more terrestrial hosts but the correlation is not as clear as in the other cases.

The prevalence of the larval acanthocephalan, Centrorhynchus (Table 6), appears sgnificantly correlated with the residence of the host in an aquatic environment. Since acanthocephalans are generally associated with a host in all stages of their life-histories, this suggests that infestation follows ingestion of an aquatic intermediate host.

The distribution of the larval mite, *Hannemania penetrans*, is erratic. Leeches were found only on the most aquatic species of host (Table 6).

SEASONAL VARIATIONS

The data presented in Tables 7-13 may be interpreted as indicating seasonal variations in some of the parasites of the Salientia studied. In many cases, however, the observed variations cannot be regarded as significantly related to seasonal changes. The attempt has been made to correlate the variations with the phases of activity of the hosts as well as the annual progression of the seasons.

The intestinal protozoa, whether considered specifically or as a group, show no marked seasonal variation. The occurrence of trypanosomes appears, however, to be correlated with the residence of the host in an aquatic environment. In hosts which are largely aquatic infestation with these flagellates was highest during the warmer months of the year. This may be due to an aquatic blood-sucking vector which feeds more actively in the warmer months of the year. This opinion is supported by the work of Franca (1908) who found that frog trypanosomes were transmitted by leeches in Europe. The haemosporidians, Karyolysus and Lankesterella, also reach a maximum in the warmer months. Miss Sanders' (1928) observations lead her to believe that Karyolysus in frogs is not transmitted by a leech but by a vector which attacks a frog but not a tadpole. Transmission of Lankesterella has been reported as being effected by the bites of leeches (Noller 1913a). It is also worthy of note that all three of the blood protozoans studied by the writer are quite generally absent from the less aquatic hosts.

Cytamoeba occurs but rarely in hosts other than *Rana sphenocephala* and reaches its maximum in November and minimum in May. It is possible that this variation represents an adaptation to the common winter breeding habit of this host. Noller (1913) thinks that a leech is probably the vector of this parasite. The variations shown by the unidentified protozoan cysts in the muscles of the bullfrog are erratic.

Trematodes of the genus Glypthelmins, which were found in the bullfrog and in the spring-peeper, failed to show significant correlations with seasonal variations. Lung flukes, however, appeared to bear out the contention of Ward (1909) that the parasites of *Rana pipiens* are lost at the time of spawning and that new infestations gradually increase to a maximum at the time of hibernation. Krull (1931) also has observed that frogs annually lose their lung flukes and take on fresh infestations.

The variations shown by bladder flukes appear to indicate that their prevalence is associated with the residence of the host in an aquatic habitat and with higher temperatures. The terrestrial toad harbored these flukes chiefly in the months following the breeding season. The bullfrog had a maximum infestation in midsummer and the southern leopard-frog was infested only at the time of breeding. Small bullfrogs were infested only in March and August.

The occurrence of Diplodiscus, while somewhat erratic, tends in the case of the large bullfrogs, to bear out the previously cited contention of Ward. The evidence, however, is by no means clear cut and is especially weak regarding the time of loss of the parasites. The appearance of this fluke in *Rana sphenocephala, Hyla crucifer* and *Pseudacris brimleyi* after these species have left the breeding places supports the belief that infestation follows ingestion of molted skin containing metacercariae. If these metacercariae accumulate on the skin during the breeding season, infestation would be expected following the first molt thereafter.

Brachycoelium occurred regularly only in the chorus-frog. The prevalence of this parasite appears to be correlated with the residence of the host in an aquatic environment. The life-history of the fluke is unknown but an aquatic secondary host probably is necessary.

When all marital flukes are considered it appears that the variation is quite erratic. Only the southern leopard-frog, which is closely related to *Rana pipiens*, shows variations which are in substantial agreement with the theories of Ward. The prevalence of larval flukes is generally erratic.

Adult cestodes reached a maximum shortly after the breeding season of each host species infested. The data suggest the agency of an aquatic intermediate host for both *Ophiotaenia saphena* and *Distoichometra bufonis*. Thomas (1931) has found that frogs become infested with *O. saphena* by ingesting copepods but the life-history of Distoichometra is unknown.

Encysted larval proteocephalids were very erratic but showed a tendency to become more abundant during the hosts residence in an aquatic environment, especially in those species which harbored few of these parasites.

The nematodes in general show erratic variation. Oswaldocruzia in the less aquatic hosts appeared to be more prevalent after the host had spent some time in an aquatic environment. The prevalence of Foleyella and Microfilaria showed minima at the time of breeding with maxima before the breeding seasons, thus being in agreement with Ward's theories.

Leeches were found only in midsummer and mites were erratic in their occurrence.

VARIATION OF PARASITES WITH SIZE AND AGE OF HOST

The data presented in the section on Parasites of Hosts Examined indicate important differences in infestation of large bullfrogs as compared with that of smaller and presumably younger individuals. The large *Rana catesbeiana* were infested with ten species of protozoans but only eight species were harbored by the individuals under 100 mm. in length. Each size group was infested by the same species of trematodes but these parasites were much more often found in the large individuals. The percentage of infestation and average number of parasites 100 per cent and 47.3 in the large bullfrogs

and 89.4 per cent and 10.42 in the small individuals. Adult cestodes were found only in the large hosts but larval cestodes occurred in both groups of bullfrogs. The percentage of infestation and average number of parasites of the latter type were 42.4 per cent and 32.5 in the large bullfrogs and 42.2 per cent and 3.58 in the small individuals. Nematodes were more common in large individuals (14 species, 100%, 166.0 average) than in small (8 species, 60.6%, 1.63 average). The larval acanthocephalan, Centrorhynchus, infested both large (78.8%, 12.6 average) and small (5.25%, 0.303 average) bullfrogs. Leeches were found attached to both large (12.1%, 0.303 average) and small (5.25%, 0.079 average) individuals. Hannemania (12.1%, 0.243 average) was restricted to large bullfrogs. Considering all metazoan parasites, the large *Rana catesbeiana* showed 100 per cent infestation and 259.2 average number of parasites per host while the small individuals were 97.4 per cent infested and harbored an average number of 15.8 parasites per host.

HOST SPECIFICITY

The parasites found offer little or no evidence of a strict host specificity in the Salientia examined. Of the fifty-six species of parasites found only sixteen were restricted to a single host, i.e. *Glypthelmins* sp., *G. subtropica, Haematoloechus longiplexus, H. breviplexus, Ostiolum complexus, Gorgoderina translucida, G. simplex, Oswaldocruzia leidyi, Macrodella ditetra, Diplodiscus intermedius, Opalina kennicotti, Cephalogonimus americanus, Ophiotaenia saphena, Spironoura catesbeianae, Oxysomatium longicaudata,* and *Spiroxys* sp. were found associated with only one of the six species studied. All of these parasites with the likely exception of the probably undescribed *Glypthelmins* sp. and *Spiroxys* sp., have, however, been recorded from other hosts by a number of authors. It follows, then, that the parasites of the North Carolina Salientia studied show little or no host specificity.

MULTIPLE INFESTATION

Multiple infestation is of common occurrence in the Salientia examined by the author. A few cases selected to show the extent of this phenomenon are presented in Table 15. This table shows that single individuals of *Scaphiopus holbrookii* and *Hyla crucifer* harbor as many as seven species of parasites. Two *Bufo fowleri* each contained eight species of parasites and one *Pseudacris brimleyi* contained seven. One individual of *Rana sphenocephala* and one of *R. catesbeiana* harbored thirteen and seventeen species of parasites respectively.

NEW SPECIES, NEW HOSTS

Three new species of parasites were found during the course of this study. These are a trematode of the genus Glypthelmins and two nematodes of the genera Spiroxys and Dujardinia. A fourth, a larval acanthocephalan of the

genus Centrorhynchus, is of uncertain status. The new species will be described in a separate paper. The genus Glypthelmins is known from a number of North American frogs but adult Spiroxys have been found in frogs only of Asiatic Rana. Hedrick (1935) has reported the larvae of Spiroxys in American frogs. Dujardinia has been reported from a toad, *Bufo marinus*, by Pearse (1936).

The following are the writer's new host records:

Scaphiopus holbrookii;

Nyctotherus cordiformis, Octomitus intestinalis, Opalina carolinensis, O. triangulata, Distoichometra bufonis, Proteocephalid cysts, *Agamonema* sp., *Cosmocercoides dukae, Oswaldocruzia leidyi, O. pipiens, Physaloptera* sp., *Rhabdias ranae;*

Bufo fowleri;

Nyctotherus cordiformis, Octomitus intestinalis, Opalina triangulata, O. virguloidea, Trichomonas augusta, Trypanosoma rotatorium, Brachycoelium hospitale, Gorgodera amplicava, Gorgoderina attenuata, G. simplex, G. translucida, Trematode cysts, *Distoichometra bufonis,* Proteocephalid cysts, *Agamonema* sp., *Cosmocercoides dukae, Oswaldocruzia pipiens, Physaloptera* sp., *Rhabdias ranae, Centrorhynchus, Hannemania penetrans;*

Pseudacris brimleyi;

Nyctotherus cordiformis, Octomitus intestinalis, Opalina chorophili, O. hylaxena, O. oblanceolata, O. obtrigonoidea, O. pickeringii, O. virguloidea, Trichomonas augusta, Trypanosoma rotatorium, Brachycoelium hospitale, Diplodiscus temperatus, Trematode cysts, *Agamascaris odontocephala, Agamonema* sp., *Cosmocercoides dukae, Oswaldocruzia pipiens, Physaloptera* sp., *Rhabdias ranae, Centrorhynchus* sp.;

Hyla crucifer;

Nyctotherus cordiformis, Octomitus intestinalis, Opalina chorophili, O. hylaxena, O. virguloidea, Trichomonas augusta, Trypanosoma rotatorium, Brachycoelium hospitale, Diplodiscus temperatus, Glypthelmins, Trematode cysts, Proteocephalid cysts, *Agamascaris odontocephala, Agamonema* sp., *Cosmocercoides dukae, Oswaldocruzia pipiens, Physaloptera* sp., *Rhabdias ranae, Centrorhynchus* sp.;

Rana catesbeiana;

Entamoeba ranarum, Leptotheca ohlmacheri, Octomitus intestinalis, Loxogenes bicolor, Ophiotaenia saphena, Proteocephalid cysts, *Dujardinia* sp., *Oxysomatium longicaudata, Physaloptera* sp., *Spiroxys* sp., *Centrorhynchus* sp., *Macrobdella ditetra, Hannemania penetrans;*

Rana sphenocephala;

Cytamoeba bacterifera, Entamoeba ranarum, Karyolysus sp., *Lankesterella* sp., *Leptotheca ohlmacheri, Nyctotherus cordiformis, Octomitus intestinalis,*

Opalina kennicotti, O. obtrigonoidea, Trichomonas augusta, Cephalogonimus americanus, Gorgoderina attenuata, Loxogenes bicolor, Ostiolum complexus, Trematode cysts, Proteocephalid cysts, *Agamascaris odontocephala, Agamonema* sp., *Dujardinia* sp., *Foleyella americana, F. ranae, Microfilaria* sp., *Centrorhynchus* sp., *Hannemania penetrans.*

SUMMARY

1. Periodic examinations on 71 bullfrogs, 60 southern leopard-frogs, 62 Fowler's toads, 60 spadefoots, 55 chorus-frogs, and 60 spring-peepers were made during the course of a year.

2. Salientians habitually residing in aquatic habitats were more often parasitized with blood protozoans, trematodes, acanthocephalans and leeches.

3. Seasonal periodicity was observed only in relatively few of the parasites found.

4. Larger, and presumably older, bullfrogs harbored considerably greater numbers of parasites than smaller individuals.

5. Few of the parasites observed occur in a single host.

6. Multiple infestations are common in the salientians studied. As many as seventeen species of parasites were found in a single bullfrog.

7. The total number of parasite species distinguished in each of the six salientian hosts studied were: *Rana catesbeiana,* 35; *Rana sphenocephala,* 30; *Bufo fowleri,* 22; *Scaphiopus holbrookii,* 15; *Pseudacris brimleyi,* 20; and *Hyla crucifer,* 21.

TABLE 1. Showing seasonal distribution of salientians examined for parasites, 1934-1935. Figures show number of hosts examined.

Species	January	February	March	April	May	June	July	August	September	October	November	December	Total
Rana catesbeiana over 100 mm.	0	4	1	4	2	5	3	1	1	0	2	10	33
Rana catesbeiana under 100 mm.	10	0	4	1	3	0	2	4	4	5	5	0	38
Rana catesbeiana all sizes	10	4	5	5	5	5	5	5	5	5	7	10	71
Rana sphenocephala	5	5	5	5	5	5	5	5	5	5	5	5	60
Bufo fowleri	15	4	5	5	5	5	5	5	5	5	2	1	62
Scaphiopus holbrookii	11	4	5	5	5	5	5	5	5	5	5	0	60
Pseudacris brimleyi	8	3	5	5	5	1	3	5	0	10	7	3	55
Hyla crucifer	9	5	5	5	5	1	5	5	0	2	8	10	60

TABLE 2. Protozoan Parasites of Salientians. Figures indicate percentage of hosts infested.

Host	Blood Protozoa	Trypanosoma	Karyolysus & Lankesterella	Cytamoeba	Intestinal Protozoa	Intestinal Ciliates	Intestinal Flagellates
Rana catesbeiana over 100 mm.	33.3	9.13	24.2	6.06	96.8	9.09	96.8
Rana catesbeiana under 100 mm.	13.2	10.5	5.25	0.0	100.0	0.0	100.0
Rana sphenocephala	71.7	38.3	28.3	40.0	96.7	38.3	93.3
Bufo fowleri	3.21	3.21	0.0	0.0	96.8	51.7	96.8
Scaphiopus holbrookii	0.0	0.0	0.0	0.0	94.5	65.1	83.7
Pseudacris brimleyi	1.8	1.8	0.0	0.0	92.7	83.7	65.5
Hyla crucifer	5.0	5.0	0.0	0.0	98.3	86.7	86.7

TABLE 3. Trematode Parasites of Salientians. The upper figures indicate percentage of hosts infested and the lower figures average number of parasites per individual.

Host	Lung Flukes	Intestinal Flukes	Bladder Flukes	All Marital Flukes	Larval Flukes	All Flukes
Rana catesbeiana over 100 mm.	60.7 2.09	94.0 12.2	72.7 10.0	100.0 24.2	69.7 23.1	100.0 47.3
Rana catesbeiana under 100 mm.	18.4 0.42	73.7 3.13	7.91 0.158	84.3 3.7	63.2 6.72	89.4 10.42
Rana sphenocephala	56.7 5.72	45.0 1.11	5.0 0.083	56.7 7.0	53.3 37.8	88.3 44.8
Bufo fowleri	0.0 0.0	1.61 0.016	8.07 0.129	8.07 0.145	21.0 0.58	29.1 0.726
Pseudacris brimleyi	0.0 0.0	76.4 6.74	0.0 0.0	76.4 6.74	3.6 2.38	76.4 9.13
Hyla crucifer	0.0 0.0	26.7 2.02	0.0 0.0	26.7 2.02	3.33 0.033	30.0 2.05

TABLE 4. Cestode Parasites of Salientians.* The upper figures indicate percentage of hosts infested and the lower figures average number of parasites per individual.

Hosts	Adult Cestodes	Larval Cestodes	All Cestodes
Rana catesbeiana, over 100 mm.	9.09 0.091	42.4 32.5	48.5 32.6
Rana catesbeiana, under 100 mm.	0.0 0.0	42.2 3.58	42.2 3.58
Rana sphenocephala	0.0 0.0	51.7 10.0	51.7 10.0
Bufo fowleri	40.3 1.97	3.21 1.61	43.6 3.58
Scaphiopus holbrookii	16.7 0.92	1.7 0.33	18.3 1.25
Hyla crucifer	0.0 0.0	3.33 0.134	3.33 0.134

* *Pseudacris brimleyi* harbored no cestodes.

TABLE 5. Nematode Parasites of Salientians. The upper figures indicate percentage of hosts infested and the lower figures average number of parasites per individual.

Host	Intestinal Nematodes	Lung Nematodes	Encysted Nematodes	Intestinal Oxyuroids	Intestinal Strongyloids	Filaroids	All Nematodes
Rana catesbeiana over 100 mm.	81.8 33.3	12.1 0.182	96.9 132.4	81.8 33.15	9.1 0.053	54.6 3.7	100.0 166.0
Rana catesbeiana under 100 mm.	21.1 0.395	15.8 0.237	23.7 0.527	5.25 0.053	18.4 0.342	2.63 0.0263	60.6 1.63
Rana sphenocephala	48.3 2.26	48.3 2.48	76.7 5.77	3.33 0.083	48.3 2.18	33.3 1.03	95.0 19.3
Bufo fowleri	72.6 4.0	1.61 0.048	42.5 15.8	32.3 0.5	61.3 3.5	0.0 0.0	91.8 19.5
Scaphiopus holbrookii	75.0 11.8	1.7 0.017	26.7 5.62	71.7 10.0	43.3 1.75	0.0 0.0	83.3 17.6
Pseudacris brimleyi	87.3 3.78	41.8 0.8	10.9 0.49	80.0 2.66	40.0 1.05	0.0 0.0	91.0 5.47
Hyla crucifer	18.4 0.784	3.33 0.083	25.0 7.5	16.7 0.234	8.33 0.55	0.0 0.0	41.7 8.4

TABLE 6. Acanthocephala, Hirudinea, and Acarina.* Upper figures indicate percentage of hosts infested and the lower figures the average number of parasites per individual.

Host	Centrorhynchus	Macrobdella	Hannemania
Rana catesbeiana, over 100 mm.	78.8 12.6	12.1 0.303	12.1 0.243
Rana catesbeiana, under 100 mm.	5.25 0.132	5.25 0.079	0.0 0.0
Rana sphenocephala	28.3 2.62	0.0 0.0	6.67 0.1
Bufo fowleri	1.61 0.0161	0.0 0.0	4.83 0.145
Pseudacris brimleyi	7.3 0.127	0.0 0.0	0.0 0.0
Hyla crucifer	1.67 0.0167	0.0 0.0	0.0 0.0

* None of these parasites were harbored by *Scaphiopus holbrookii*.

TABLE 7. Seasonal Variation of Parasites. *Rana catesbeiana* (over 100 mm.). The first figures indicate percentage of infestation, the second, when given, indicate average number of parasites per individual.

Phase	Pre-breeding	Breeding	Post-breeding	Autumn	Hibernating
Average Date	Feb. 10	April 28	July 6	Oct. 10	Dec. 16
Range of Dates	Feb. 10	Mar.28-June 6	June28–July22	Aug.29 -Nov.9	Dec. 16
No. Exam.	4	8	7	4	10
Aver. Length mm.	139.5	139.2	127.1	134.1	160.2
Cytamoeba	25.0	0.0	0.0	0.0	10.0
Entamoeba	0.0	12.5	0.0	0.0	0.0
Protozoan cysts in muscles	25.0	37.5	14.3	75.0	60.0
Karyolysus or Lankesterella	0.0	25.0	28.6	25.0	30.0
Leptotheca	0.0	0.0	0.0	25.0	0.0
Nyctotherus	25.0	12.5	0.0	25.0	0.0
Octomitus	100.0	62.5	85.7	100.0	90.0
Trichomonas	100.0	100.0	100.0	75.0	100.0
Trypanosoma	0.0	12.5	28.6	0.0	0.0
All Intestinal Flagellates	100.0	100.0	100.0	100.0	100.0
All Intestinal Protozoa	100.0	100.0	100.0	100.0	100.0
All Blood Protozoa	25.0	25.0	57.2	25.0	30.0
All Protozoa	100.0	100.0	100.0	100.0	100.0
Diplodiscus	75.0	25.0	85.7	75.0	100.0
	4.25	2.75	2.85	15.0	12.1
Bladder Flukes	25.0	87.5	100.0	75.0	60.0
	0.25	11.13	21.7	14.5	3.7
Glypthelmins	50.0	62.5	28.6	0.0	90.0
	5.0	2.75	0.428	0.0	8.8
Haematoloechus	75.0	25.0	71.4	75.0	70.0
	2.75	0.25	1.29	6.25	2.2
Loxogenes	0.0	37.5	28.6	50.0	50.0
	0.0	2.37	2.14	1.75	0.8

TABLE 7, continued.

Phase	Pre-breeding	Breeding	Post-breeding	Autumn	Hibernating
Average Date	Feb. 10	April 28	July 6	Oct. 10	Dec. 16
Range of Dates	Feb. 10	Mar.28-June 6	June28-July22	Aug.29 -Nov.9	Dec. 16
No. Exam.	4	8	7	4	10
Aver. Length mm.	139.5	139.2	127.1	134.1	160.2
Encysted Flukes	75.0	62.5	71.4	50.0	100.0
	14.5	37.5	14.9	12.3	31.6
All Marital Flukes	100.0	100.0	100.0	100.0	100.0
	12.25	19.25	28.41	37.5	27.6
All Flukes	100.0	100.0	100.0	100.0	100.0
	26.75	56.75	43.31	49.8	59.2
Ophiotaenia	0.0	25.0	14.3	0.0	0.0
	0.0	0.25	0.143	0.0	0.0
Proteocephalid	25.0	25.0	0.0	50.0	90.0
Cysts	1.0	26.25	0.0	95.8	47.6
All Cestodes	25.0	37.5	14.3	50.0	90.0
	1.0	26.5	0.143	95.8	47.6
Agamascaris	0.0	12.5	57.2	50.0	70.0
	0.0	0.125	0.714	1.5	1.1
Agamonema	100.0	87.5	85.7	75.0	100.0
	78.25	44.8	35.9	180.5	254.6
Cosmocercoides	0.0	62.5	0.0	25.0	0.0
	0.0	5.37	0.0	0.5	0.0
Dujardinia	50.0	25.0	0.0	0.0	30.0
	3.0	0.375	0.0	0.0	1.0
Foleyella	25.0	50.0	14.3	75.0	90.0
	1.0	4.5	0.286	5.25	6.1
Oswaldocruzia	0.0	25.0	0.0	25.0	0.0
	0.0	0.375	0.0	0.25	0.0
Oxysomatium	75.0	37.5	28.6	0.0	0.0
	6.25	17.5	5.57	0.0	0.0
Physaloptera	0.0	25.0	71.4	50.0	50.0
	0.0	0.5	3.0	1.0	2.7
Rhabdias in lungs	0.0	12.5	14.3	50.0	0.0
	0.0	0.125	0.286	0.75	0.0
Rhabdias in body	0.0	0.0	0.0	25.0	0.0
cavity	0.0	0.0	0.0	0.5	0.0
Spironoura	0.0	50.0	42.8	50.0	60.0
	0.0	63.62	29.71	41.0	4.2
Spiroxys	0.0	12.5	28.6	0.0	0.0
	0.0	0.25	3.0	0.0	0.0
All Nematodes in	100.0	87.5	85.7	100.0	100.0
Definitive Host	7.25	92.24	41.85	49.25	13.0
All Encysted	100.0	100.0	100.0	75.0	100.0
Nematodes	81.25	45.3	36.6	182.0	256.7
All Nematodes	100.0	100.0	100.0	100.0	100.0
	88.5	137.5	78.45	231.3	269.7
Centrorhynchus	75.0	87.5	57.2	75.0	100.0
	3.75	22.0	8.86	10.0	16.5
Macrobdella	0.0	0.0	57.2	0.0	0.0
	0.0	0.0	1.43	0.0	0.0
Hannemania	0.0	0.0	42.8	25.0	0.0
	0.0	0.0	0.714	0.75	0.0
All Metazoans	100.0	100.0	100.0	100.0	100.0
	112.3	209.9	132.9	387.7	393.9

TABLE 8. Seasonal Variation of Parasites. *Rana catesbeiana* (under 100 mm.). The first figure indicates percentage of infestation, the second, when given, indicates average number of parasites per individual.

Phase	Midwinter	Spring	Early Summer	Late Summer	Autumn
Average Date	Jan. 10	Mar. 22	May 25	Aug. 22	Oct. 28
Range of Dates	Jan. 10	Mar. 4-Apr. 27	May22-May28	Jul.22-Sept. 30	Oct.11-Nov.29
No. Exam.	10	5	3	10	10
Aver. Length mm.	36.0	49.0	64.9	48.9	41.8
Entamoeba	30.0	0.0	33.3	0.0	10.0
Karyolysus or Lankesterella	0.0	0.0	33.3	10.0	0.0
Leptotheca	70.0	0.0	0.0	10.0	50.0
Octomitus	90.0	100.0	100.0	100.0	100.0
Trichomonas	70.0	80.0	100.0	90.0	50.0
Trypanosoma	0.0	0.0	33.3	20.0	10.0
Unidentified Flagellates	0.0	40.0	33.3	20.0	10.0
All Blood Protozoa	0.0	0.0	33.3	30.0	10.0
All Intestinal Flagellates	100.0	100.0	100.0	100.0	100.0
All Protozoa	100.0	100.0	100.0	100.0	100.0
Bladder Flukes	0.0	20.0	0.0	20.0	0.0
	0.0	0.2	0.0	0.5	0.0
Diplodiscus	70.0	0.0	100.0	30.0	50.0
	1.4	0.0	4.0	3.4	1.2
Glypthelmins	0.0	20.0	0.0	0.0	0.0
	0.0	3.0	0.0	0.0	0.0
Haematoloechus	10.0	40.0	0.0	20.0	20.0
	0.1	0.4	0.0	0.6	0.7
Loxogenes	40.0	40.0	100.0	30.0	60.0
	0.7	0.6	2.33	0.8	1.1
All Marital Flukes	80.0	80.0	100.0	80.0	90.0
	2.2	4.2	6.33	5.3	3.0
Encysted Flukes	50.0	80.0	100.0	40.0	80.0
	7.8	23.0	17.0	3.1	1.9
All Flukes	80.0	100.0	100.0	80.0	100.0
	6.1	27.2	23.3	8.2	4.7
Proteocephalid Cysts	50.0	40.0	33.3	50.0	30.0
	2.6	8.6	7.33	4.0	0.5
Agamascaris	0.0	20.0	0.0	0.0	0.0
	0.0	0.2	0.0	0.0	0.0
Agamonema	20.0	20.0	33.3	30.0	0.0
	0.2	0.4	3.0	0.5	0.0
Cosmocercoides	0.0	20.0	0.0	0.0	0.0
	0.0	0.2	0.0	0.0	0.0
Foleyella	0.0	20.0	0.0	0.0	0.0
	0.0	0.2	0.0	0.0	0.0
Oswaldocruzia	10.0	60.0	0.0	10.0	20.0
	0.2	1.4	0.0	0.2	0.2
Rhabdias in lungs	0.0	20.0	0.0	40.0	10.0
	0.0	0.2	0.0	0.7	0.1
Rhabdias in body Cavity	30.0	0.0	0.0	20.0	30.0
	0.3	0.0	0.0	0.7	0.8
Spironoura	0.0	0.0	0.0	10.0	0.0
	0.0	0.0	0.0	0.1	0.0
All Nematodes in Definitive Host	40.0	80.0	0.0	60.0	60.0
	0.5	2.0	0.0	1.7	1.1
All Encysted Nematodes	20.0	40.0	33.3	30.0	0.0
	0.2	0.6	3.0	0.5	0.0
All Nematodes	40.0	100.0	33.3	70.0	60.0
	0.7	2.6	3.0	2.2	1.1
Centrorhynchus	0.0	20.0	0.0	10.0	0.0
	0.0	0.2	0.0	0.4	0.0
Macrobdella	0.0	0.0	0.0	20.0	0.0
	0.0	0.0	0.0	0.3	0.0
All Metazoans	90.0	100.0	100.0	100.0	100.0
	9.4	38.6	33.7	15.1	6.3

TABLE 9. Seasonal Variation of Parasites. *Rana sphenocephala.* The first figure indicates percentage of infestation, the second, when given, indicates average number of parasites per individual.

Phase	Breeding	Post-breeding	Midsummer	Early Winter
Average Date	Feb. 9	May 14	Aug. 15	Nov. 12
Range of Dates	Jan. 10-Mar. 4	Apr. 18-June 6	July 6-Sept. 9	Oct. 11-Dec. 21
No. Exam.	15	15	15	15
Average Length mm.	55.9	55.1	53.4	56.0
Cytamoeba	53.3	6.67	40.0	60.0
Entamoeba	6.67	0.0	0.0	0.0
Karyolysus or Lankesterella	20.0	26.7	40.0	26.7
Leptotheca	20.0	0.0	0.0	20.0
Nyctotherus	6.67	13.3	20.0	13.3
Octomitus	100.0	93.3	80.0	93.3
Opalina	40.0	46.7	20.0	13.3
Trichomonas	86.7	80.0	86.7	60.0
Trypanosoma	13.3	46.7	53.3	40.0
All Ciliates	40.0	53.3	26.6	26.6
All Intestinal Flagellates.	100.0	93.3	86.7	93.3
All Intestinal Protozoa	100.0	100.0	93.3	96.7
All Blood Protozoa	66.7	66.7	80.0	73.3
All Protozoa	100.0	100.0	93.3	96.7
Brachycoelium	6.67	6.67	0.0	0.0
	0.067	0.8	0.0	0.0
Cephalogonimus	6.67	0.0	0.0	0.0
	0.067	0.0	0.0	0.0
Diplodiscus	26.7	20.0	60.0	53.3
	1.13	0.867	0.8	0.667
Gorgoderina	13.3	6.67	0.0	0.0
	0.2	0.133	0.0	0.0
Loxogenes	0.0	6.67	6.67	6.67
	0.0	0.267	0.067	0.067
Ostiolum	33.3	66.7	66.7	66.7
	1.73	3.53	3.07	14.53
Encysted Flukes	33.3	46.7	66.7	66.7
	38.9	53.3	40.2	18.5
All Flukes in Definitive Host	60.0	66.7	80.0	86.7
	3.2	5.6	3.93	15.27
All Flukes	66.7	100.0	93.3	93.3
	42.1	58.9	44.13	33.77
Proteocephalid Cysts	40.0	53.3	76.7	40.0
	11.8	10.5	9.73	8.07
Agamascaris	26.7	6.67	6.67	33.3
	1.33	0.067	0.067	0.467
Agamonema	53.3	46.7	60.0	93.3
	4.33	2.6	1.4	8.27
Cosmocercoides	13.3	0.0	0.0	0.0
	0.33	0.0	0.0	0.0
Dujardinia	6.67	6.67	6.67	0.0
	0.067	0.267	0.133	0.0
Foleyella	26.7	26.7	33.3	46.7
	0.533	0.333	1.13	2.13
Microfilaria	0.0	6.67	6.67	13.3
Oswaldocruzia	66.7	40.0	33.3	53.3
	3.4	2.8	0.533	2.0
Rhabdias in lungs	60.0	33.3	46.7	53.3
	4.73	2.03	1.73	1.4
Rhabdias in body cavity	80.0	46.7	26.7	80.0
	19.1	0.867	0.333	14.7
All Intestinal Nematodes	66.7	40.0	33.3	53.3
	3.73	2.8	0.533	2.0
All Nematodes in Definitive Host	93.3	86.7	73.3	93.3
	28.13	6.07	3.73	20.23
All Encysted Nematodes	60.0	60.0	60.0	93.3
	5.73	2.93	1.6	8.74
All Nematodes	100.0	93.3	86.7	100.0
	33.86	9.0	5.33	28.97
Centrorhynchus	40.0	26.7	20.0	26.7
	1.67	7.34	0.533	0.867
Hannemania	6.67	13.3	0.0	6.67
	0.0133	0.2	0.0	0.067
All Metazoans	100.0	100.0	100.0	100.0
	89.44	85.97	59.72	71.75

TABLE 10. Seasonal Variation of Parasites. *Bufo fowleri.* The first figure indicates percentage of infestation, the second, when given, indicates average number of parasites per individual.

Phase	Hibernation	Emergence and Breeding	Midsummer	Pre-hibernation
Average Date	Jan. 15	May 1	Aug. 2	Oct. 24
Range of Dates	Dec. 29-Feb. 14	Mar. 28-June 7	July 6-Sept. 7	Oct. 10-Nov. 23
No. Exam.	20	20	15	7
Average Length mm.	48.9	48.9	47.1	48.3
Nyctotherus	30.0	25.0	53.3	42.8
Octomitus	60.0	60.0	40.0	42.8
Opalina	25.0	20.0	26.7	71.4
Trichomonas	90.0	95.0	93.3	100.0
Trypanosoma	0.0	0.0	13.3	0.0
All Ciliates	45.0	35.0	66.7	85.6
All Intestinal Flagellates.	95.0	100.0	93.3	100.0
All Intestinal Protozoa.	95.0	100.0	93.3	100.0
All Protozoa	95.0	100.0	93.3	100.0
Bladder Flukes	5.0	5.0	13.3	14.3
	0.1	0.1	0.2	0.143
Brachycoelium	0.0	0.0	0.0	14.3
	0.0	0.0	0.0	0.143
All Marital Flukes	5.0	5.0	13.3	14.3
	0.1	0.1	0.2	0.286
Encysted Flukes	10.0	35.0	13.3	28.6
	0.6	0.5	0.6	0.714
All Flukes	15.0	40.0	26.7	42.8
	0.7	0.6	0.8	1.0
Distoichometra	30.0	40.0	53.3	42.8
	1.2	2.1	3.33	0.856
Proteocephalid Cysts	0.0	0.0	13.3	0.0
	0.0	0.0	6.67	0.0
All Cestodes	30.0	40.0	66.7	42.8
	1.2	2.1	10.0	0.856
Agamonema	55.0	45.0	26.7	57.2
	34.0	3.95	12.75	4.14
Cosmocercoides	15.0	45.0	40.0	14.3
	0.15	0.8	0.6	0.286
Oswaldocruzia	35.0	65.0	86.7	71.4
	0.8	3.85	2.8	7.86
Physaloptera	0.0	0.0	6.67	0.0
	0.0	0.0	0.067	0.0
Rhabdias in lungs	0.0	0.0	0.0	14.3
	0.0	0.0	0.0	0.428
Rhabdias in body cavity.	0.0	5.0	0.0	0.0
	0.0	0.1	0.0	0.0
All Intestinal Nematodes	45.0	80.0	100.0	71.4
	0.95	4.65	3.47	8.15
All Nematodes in Definitive Host	45.0	80.0	100.0	71.4
	0.95	4.75	3.47	8.56
All Nematodes	75.0	100.0	100.0	100.0
	34.95	8.7	16.2	12.7
Centrorhynchus	0.0	0.0	6.67	0.0
	0.0	0.0	0.067	0.0
Hannemania	0.0	5.0	13.3	0.0
	0.0	0.05	0.533	0.0
All Metazoans	90.0	100.0	100.0	100.0
	36.85	11.45	27.6	14.6

TABLE 11. Seasonal Variation of Parasites. *Scaphiopus holbrookii.* The upper figure indicates percentage of infestation, the lower, when given, indicates average number of parasites per individual.

Phase	Hibernating	Breeding	Early Summer	Late Summer	Autumn
Average Date	Jan. 9	Mar. 16	May 30	Aug. 7	Oct. 10
Range of Dates	Jan. 3-Jan. 10	Feb.25-Apr.12	May15-June 6	July20-Aug.26	Sept.16-Nov.4
No. Exam.	11	14	10	10	15
Aver. Length mm.	43.7	55.5	53.7	44.9	54.6
Nyctotherus	54.5	50.0	60.0	50.0	73.4
Octomitus	81.7	42.8	50.0	80.0	66.7
Opalina	36.4	21.4	10.0	30.0	40.0
Trichomonas	91.0	57.2	80.0	80.0	80.0
All Ciliates	72.7	57.2	60.0	50.0	80.0
All Flagellates	100.0	64.3	90.0	80.0	86.7
All Protozoa	100.0	85.7	100.0	80.0	100.0
Distoichometra	9.1	28.6	20.0	0.0	20.0
	0.46	1.78	1.7	0.0	0.53
Proteocephalid	0.0	0.0	10.0	0.0	0.0
Cysts	0.0	0.0	2.0	0.0	0.0
All Cestodes	9.1	28.6	30.0	0.0	20.0
	0.46	1.78	3.7	0.0	0.53
Agamonema	9.1	14.3	40.0	30.0	40.0
	0.09	0.71	3.1	27.8	1.13
Cosmocercoides	72.7	78.6	70.0	70.0	66.7
	3.37	15.85	3.5	19.6	7.34
Oswaldocruzia	27.3	64.3	60.0	50.0	20.0
	0.46	1.57	2.8	3.6	0.93
Physaloptera	0.0	0.0	0.0	0.0	13.3
	0.0	0.0	0.0	0.0	0.8
Rhabdias in lungs	9.1	0.0	0.0	0.0	0.0
	0.09	0.0	0.0	0.0	0.0
Rhabdias in body	9.1	0.0	0.0	0.0	0.0
cavity	0.09	0.0	0.0	0.0	0.0
All Intestinal	72.7	85.7	70.0	80.0	66.7
Nematodes	3.83	17.42	6.3	23.2	9.07
All Nematodes in	72.7	85.7	70.0	80.0	66.7
Definitive Host	4.0	17.42	6.3	23.2	9.07
All Nematodes	72.7	85.7	90.0	90.0	80.0
	4.09	18.1	9.4	51.0	10.2
All Metazoans	72.7	85.7	90.0	90.0	80.0
	4.54	19.9	13.1	51.0	10.72

TABLE 12. Seasonal Variation of Parasites. *Pseudacris brimleyi.* The upper figure indicates percentage of infestation, the lower, when given, indicates average number of parasites per individual.

Phase	Pre-breeding	Breeding	Early Summer	Late Summer	Early Winter
Average Date	Jan. 11	Mar. 17	May 21	Aug. 12	Oct. 30
Range of Dates	Dec.31 -Jan.20	Feb.13 -Apr.17	Apr. 27-June 7	Jul.20 -Aug.26	Oct.10-Nov.29
No. Exam.	11	12	7	8	17
Aver. Length mm.	27.5	28.6	27.8	24.7	27.8
Nyctotherus	63.7	16.7	0.0	50.0	23.6
Octomitus	63.7	33.3	85.7	62.5	53.0
Opalina	63.7	83.4	85.7	82.5	82.4
Trichomonas	9.1	50.0	28.6	37.5	29.4
Trypanosoma	0.0	0.0	0.0	0.0	5.9
All Ciliates	81.8	83.4	85.7	82.5	82.4
All Intestinal Flagellates	72.7	50.0	85.7	75.0	58.8
All Intestinal Protozoa	100.0	100.0	85.7	82.5	88.3
All Protozoa	100.0	100.0	85.7	82.5	88.3
Brachycoelium	81.8	83.4	71.4	50.0	70.6
	6.27	14.16	5.0	3.25	4.06
Diplodiscus	0.0	8.3	14.3	12.5	0.0
	0.0	0.083	0.143	0.125	0.0
All Marital Flukes	81.8	91.7	71.4	62.5	70.6
	6.27	14.25	5.14	3.38	4.06
Encysted Flukes	9.1	0.0	14.3	0.0	0.0
	0.09	0.0	18.6	0.0	0.0
Agamascaris	0.0	8.3	0.0	0.0	0.0
	0.0	0.083	0.0	0.0	0.0
Agamonema	27.3	8.3	0.0	0.0	5.9
	2.18	0.083	0.0	0.0	0.059
Cosmocercoides	90.9	91.7	85.7	62.5	64.7
	5.45	2.92	2.43	1.25	1.35
Oswaldocruzia	90.0	33.3	28.6	12.5	29.4
	1.45	0.58	3.15	0.125	0.71
Physaloptera	9.1	0.0	0.0	0.0	5.9
	0.45	0.0	0.0	0.0	0.059
Rhabdias in lungs	54.5	58.3	42.9	12.5	35.3
	1.09	1.67	0.43	0.125	0.47
Rhabdias in body cavity	18.2	16.7	14.3	0.0	29.4
	0.45	0.33	0.29	0.0	0.6
All Intestinal Nematodes	100.0	91.7	100.0	75.0	76.5
	7.35	3.5	5.58	1.38	2.12
All Nematodes in Definitive Host	100.0	100.0	100.0	75.0	82.4
	8.91	5.5	6.28	1.5	3.18
All Encysted Nematodes	100.0	16.7	0.0	0.0	5.9
	2.2	0.17	0.0	0.0	0.06
All Nematodes	100.0	100.0	100.0	75.0	82.4
	11.1	5.66	6.28	1.5	3.24
Centrorhynchus	0.0	8.3	0.0	0.0	17.7
	0.0	0.083	0.0	0.0	0.35
All Metazoans	100.0	100.0	100.0	87.5	100.0
	17.4	20.0	30.0	4.88	7.65

TABLE 13. Seasonal Variation of Parasites. *Hyla crucifer*. The upper figure indicates percentage of infestation, the lower, when given, indicates average number of parasites per individual.

Phase	Pre-breeding	Breeding	Post-breeding	Midsummer	Early Winter
Average Date	Dec. 30	Feb. 8	May 10	July 31	Nov. 14
Range of Dates	Dec. 27-31	Jan. 1-Mar. 4	Apr. 17-June 7	Jul. 9-Aug. 26	Oct.10–Nov.29
No. Exam.	10	19	11	10	10
Aver. Length mm.	27.8	28.6	26.5	20.8	26.4
Nyctotherus	60.0	47.3	36.4	30.0	40.0
Octomitus	90.0	68.4	45.5	80.0	50.0
Opalina	90.0	100.0	91.0	70.0	70.0
Trichomonas	90.0	52.6	72.8	40.0	80.0
Trypanosoma	10.0	5.26	9.1	0.0	0.0
All Ciliates	90.0	100.0	91.0	70.0	70.0
All Intestinal Flagellates	100.0	79.0	91.0	90.0	80.0
All Intestinal Protozoa	100.0	100.0	100.0	90.0	100.0
All Protozoa	100.0	100.0	100.0	90.0	100.0
Brachycoelium	0.0	10.5	18.2	0.0	0.0
	0.0	0.32	0.36	0.0	0.0
Diplodiscus	0.0	0.0	0.0	10.0	10.0
	0.0	0.0	0.0	0.1	0.1
Glypthelmins	20.0	10.5	18.2	10.0	40.0
	2.9	0.37	0.73	0.2	6.3
All Marital Flukes	20.0	21.0	36.4	20.0	40.0
	2.9	6.8	1.1	0.3	6.4
Encysted Flukes	0.0	5.26	9.1	0.0	0.0
	0.0	0.053	0.09	0.0	0.0
All Flukes	20.0	26.3	45.5	20.0	40.0
	2.9	0.74	1.18	0.3	6.4
Proteocephalid	0.0	10.5	0.0	0.0	0.0
Cysts	0.0	0.421	0.0	0.0	0.0
Agamascaris	0.0	0.0	0.0	0.0	10.0
	0.0	0.0	0.0	0.0	0.1
Agamonema	20.0	31.6	27.3	20.0	20.0
	0.3	4.79	16.6	1.9	15.4
Cosmocercoides	10.0	10.5	9.1	30.0	10.0
	0.2	0.105	0.091	0.4	0.1
Oswaldocruzia	10.0	5.26	0.0	0.0	30.0
	0.2	0.105	0.0	0.0	2.9
Physaloptera	10.0	0.0	9.1	0.0	0.0
	0.1	0.0	0.273	0.0	0.0
Rhabdias in lungs	0.0	5.26	9.1	0.0	0.0
	0.0	0.21	0.91	0.0	0.0
Rhadias in body	0.0	5.26	0.0	0.0	0.0
cavity	0.0	0.16	0.0	0.0	0.0
All Intestinal Nematodes	20.0	15.8	18.2	20.0	30.0
	0.5	0.21	0.36	0.4	3.0
All Encysted Nematodes	20.0	31.6	27.3	20.0	30.0
	0.3	4.8	16.6	1.9	15.5
All Nematodes	40.0	42.2	36.4	50.0	40.0
	0.8	5.37	16.9	2.4	18.4
Centrorhynchus	10.0	0.0	0.0	0.0	0.0
	0.1	0.0	0.0	0.0	0.0
All Metazoans	50.0	68.4	63.6	60.0	80.0
	3.8	6.53	18.1	2.7	24.8

TABLE 14. Comparison of Parasites in Hosts of Different Habitat Preference, 1934-1935. The first figure indicates percentage of infestation, the second, when given, indicates average number of parasites per individual.

Host	Number Examined	Average Length	Blood Protozoa	Intestinal Protozoa	Trematoda	Cestoda	Nematoda	Acantho-cephala	Metazoan Parasites
Scaphiopus holbrookii	60	51.0	0.0	94.5	0.0 0.0	18.3 1.25	83.3 17.6	0.0 0.0	83.3 18.9
Bufo fowleri	62	48.5	3.21	96.8	29.1 0.73	43.6 3.58	91.8 19.6	1.61 0.016	96.8 23.9
Rana sphenocephala	60	55.1	71.7	96.7	88.3 44.8	51.7 10.0	95.0 19.3	28.3 2.62	100.0 76.9
Rana catesbeiana (large)	33	143.2	33.3	96.8	100.0 47.3	48.5 32.6	100.0 166.0	78.8 12.6	100.0 259.2
Rana catesbeiana (small)	38	44.9	13.2	100.0	89.4 10.42	42.2 3.58	60.6 1.63	5.25 0.132	97.4 15.8
Rana catesbeiana (all sizes)	71	90.2	22.5	98.6	94.3 27.6	45.1 17.1	78.9 77.9	39.4 5.93	98.6 128.9
Pseudacris brimleyi	55	27.4	1.8	92.7	76.4 9.13	0.0 0.0	91.0 5.47	7.3 0.127	95.2 14.7
Hyla crucifer	60	26.4	5.0	98.3	30.0 2.05	3.33 0.134	41.7 8.4	1.67 0.017	65.0 10.6

TABLE 15. Multiple Infestation. The figures indicate the greatest number of parasite species observed in a single individual.

Host	Protozoa	Trematoda	Cestoda	Nematoda	Acantho-cephala	Annelida	Arthropoda	All Parasites
Scaphiopus holbrookii	4	0	1	4	0	0	0	7
Hyla crucifer	5	2	1	4	1	0	0	7
Bufo fowleri	5	3	1	3	1	0	1	8
Pseudacris brimleyi	4	3	0	5	1	0	0	9
Rana sphenocephala	6	5	1	5	1	0	1	13
Rana catesbeiana	5	8	2	8	1	1	1	17

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THE EFFECT OF RAINFALL AND TEMPERATURE ON THE ANNUAL RADIAL GROWTH OF PINE IN THE SOUTHERN UNITED STATES

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THE EFFECT OF RAINFALL AND TEMPERATURE ON THE ANNUAL RADIAL GROWTH OF PINE IN THE SOUTHERN UNITED STATES

INTRODUCTION

The basic cause of the rapid growth of pine in the South is generally attributed to the warm, humid climate. Marked fluctuations of annual growth have been observed by almost everyone who has had occasion to make increment borings, or count and measure annual rings on stumps. These fluctuations in annual-ring width can often be correlated with fire damage, decrease in stand density due to cutting, and other factors. However, they are in many instances correlated with the climatic factors, rainfall, and temperature.

The influence of rainfall and temperature upon the radial growth of four species of pine has been evaluated and some of the outstanding correlations are given in this paper. The specific objective of the work was to find a satisfactory method of measuring the relationship between rainfall and temperature and growth, and to present the results of the most acceptable methods of analysis in graphic form and discuss the more outstanding correlations. The species studied and the locations where data were obtained were: loblolly pine (*Pinus taeda* L.) in southwestern Louisiana; slash pine (*P. caribaea* Morelet) and longleaf pine (*P. palustris* Mill.) in southern Georgia; and shortleaf pine (*P. echinata* Mill.) in northern Arkansas. The growth data were obtained by Jesse D. Diller of the Division of Forest Pathology, U. S. Department of Agriculture, while making a reconnaissance survey of pine-canker infection in the South. Diller made all the growth measurements and turned the data over to the writer, who has not seen the specific stands in which trees were measured. The writer is indebted to Professors R. C. Hawley and Ellsworth Huntington of Yale University, and L. H. Reineke of the Northeastern Forest Experiment Station for many helpful suggestions in the analysis.

PREVIOUS WORK

The effect of climatic change on the diameter growth of long-lived trees in semi-arid regions has been the subject of extensive study. The objectives of these studies have been aptly expressed by Douglass (1924, 1934) in the following statement: "The annual rings [of trees] at the dry borders of the southwestern forests give excellent rainfall records. This is a reaction of the tree to its environment and as such is a contribution to ecology. Climatology is closely related to the study of tree rings because long-lived trees give rainfall records for more than a thousand years past and thus supply fun-

[1] Condensed from a thesis submitted to the Faculty of the School of Forestry, Yale University, in partial fulfillment of the requirements for the degree of Master of Forestry, 1935.

damental data unequalled elsewhere in length of time and accuracy of dated record. These long records have developed the use of new and more efficient methods in the study of climatic cycles. These records of rains and droughts also meet the needs of the reclamation engineer, and the soil erosion specialist.

"Geology stands in close relation because the interpretation of modern rings in terms of climate enables us to read the meaning of fossil rings in the study of past climates. The astronomer finds in tree-ring variations a reflection of solar changes over longer periods of time than described in human history. Archaeologists have studied rings in the constructions of primitive man in which are recorded ancient rainfall conditions; by cross identification they are at times able to learn the exact time of construction of great ruins, and can often see in the droughts recorded in the annual rings of timbers a possible explanation of abandonment of habitations."

Douglass (1914, 1922) working with ponderosa pine in Arizona found that (1) variation in the annual rings of individual pine trees, in the dry regions of the northern part of the state, exhibited such uniformity that the rings of one tree could be cross-identified with rings in other trees over large areas and the date of their formation established with practical certainty, and that (2) ring thickness was proportional to rainfall with an accuracy of 70 to 85 per cent in recent years and this accuracy presumably extended over centuries, and (3) an empirical formula could be made to express the relationship between tree growth and rainfall. He found the following cycles in the 500-year record of trees near Flagstaff: an approximate 33-year cycle in the last 200 years, a 20-year cycle and a 11-year cycle in the last 400 years. The 11-year cycle showed marked relationship to the California coast rainfall and temperature, and to the sun-spot curve. He also found a still better agreement between tree growth in northern Germany (Eberswalde) and sun-spot occurrence.

Douglass (1917) observed that trees in dry climates provide a valuable record of rainfall, while trees of wet climates give better records of sun-spot activity (11-year periodicity of sun-spots).

Douglass (1909, 1919) found conifers most suitable for climatic studies because of their wide distribution, the great variety of climates in which they occur, and the prominence of the rings. The chief trees that he used were ponderosa pine, Scotch pine, Douglas fir, and Sequoia. Apparently good evidence was found to show that double rings are caused by spring droughts, and that they are indicative of the distribution of rainfall throughout the year in the southwest. Douglass also pointed to the possibility of using tree records in the intensive study of the location of homogeneous meteorological conditions and in outlining meteorological districts.

Kienholz (1934) found no correlation between meteorological conditions and double maxima in the cambial growth of young red pine in New Hamp-

shire. Cambial growth, measured by the MacDougal dendrograph, began early in May, reached a maximum June 2, decreased slightly and reached a second maximum July 9. He suggested that the first maximum was associated with the development of spring wood and the second maximum with the development of summer wood. Kienholz stressed the importance of stored foods in the rapid building of new wood in the spring. This point should be kept in mind in interpreting the reason for a positive correlation between radial growth rate, and summer rainfall of the previous year in slash pine near Waycross, Georgia.

Bogue (1905) investigated the relation between seasonal and annual growth of 27 shade and fruit trees near Stillwater, Oklahoma. Analyzing growth and climatic data for a 4-year period (1898 to 1901) he found that the month of maximum rainfall was also the month of maximum growth. On the basis of such a short time series this correlation may have been fortuitous. He also measured the rings of 42 trees for a 13-year period (1892 to 1904) at East Lansing, Michigan, and observed that an annual precipitation of 30 to 35 inches gave a ring of 0.11 to 0.15 inch wide, and that abnormally large or small rainfall was evidenced by the tree growth of the following year.

Robbins (1921) studied the relation between the growth rates of oak (largely *Quercus rubra* L., and *Q. imbricaria* Michx.) and rainfall and temperature in Missouri. Annual growth data from 16 trees, which were approximately 100 years old, were compared with climatic data from a station 1 mile away. He found the best correlation between the total rainfall for March, April, May, and June and annual radial growth. This correlation was determined graphically[2] by plotting rainfall and growth over time. Robbins found no relation between precipitation of one year and growth during the next. The average temperature of May and June was negatively correlated with growth as determined graphically. He suggests that the "building material (for new growth in the spring) comes from the assimilatory activity of the leaves and not from reserve foods." This is opposite to the suggestion of Kienholz (1934).

Burns (1929) considered it impossible to correlate ring width with the climatic factors because of the phenomenon of eccentric growth, the variation in width of a single ring at different elevations on the trunk, and the suppression of rings near the base of the tree. He believed that the *source*, *time*, and *nature* of precipitation was immaterial, but that the essential condition was that available moisture be present around the tree roots during the season when temperature conditions are favorable for growth. Apparently he gave considerable weight to surface and subsurface lateral movement of water in the soil. The concentration of tree roots in the A horizon of most forest

[2] In the writer's experience it has been extremely difficult, if not impossible, to isolate by graphic means the period of rainfall that shows the best association with growth.

soils indicates to the writer the great importance of an immediate aerial source of soil moisture and not laterally translocated moisture.

The effect of rainfall and temperature on the diameter growth of longleaf pine in western Florida was studied by Lodewick (1930), working in the Choctawhatchee National Forest in western Florida about 7 miles from the Gulf of Mexico. The region receives about 60 inches of rainfall a year, and the soil on which the study-trees were located was deep Norfolk sand. Fifty-seven trees, ranging in diameter from 2 to 19 inches at breast height were measured. The time series involved was 12 years. The data were analyzed by graphic methods. Rainfall during the latter part of the growing season (from June 1 or July 1 until October 15) exerted the principal controlling influence on summer wood formation. Rainfall accompanying the period of spring wood formation showed a fair correlation with the width of the spring wood, but the correlation was poorer than that for the summer wood. He found the width of spring wood over a number of years to be almost constant irrespective of rainfall. Lodewick states "vigorous trees were better visual indicators of the effect of climatic factors on wood production than were non-vigorous trees, since the sinuosities of their growth curves were more marked." This is opposite to the findings of Douglass, although each worked with different trees in different climates. Lodewick found little or no association between temperature and growth.

Exception is taken by Lyon (1935) to the work and conclusions of Burns (1929) because the latter used such a short time series, 12 years, and because of the youthfulness of the trees (white pine under 10 inches in diameter). Lyon's contention is that the growth rings of young trees are complacent, that is, they apparently do not respond to changes in single environmental factors. The inference is that the annual growth of rapidly growing trees is much less affected by deviations of rainfall and temperature than the annual growth of slowly growing trees, which may be true for hemlock in New Hampshire; but it is in opposition to the findings of Lodewick (1930) in western Florida, and to the observations of the writer in Georgia, Louisiana, and northern Arkansas.

Diller (1935) studied the relation of temperature and precipitation to the growth of beech in northern Indiana. He measured the annual growth of 10 trees in each of seven woodlands, and correlated it with climatic data for the period of 1913 to 1933. Annual variations in the width of rings for the period were correlated inversely with the average temperature for the month of June. In some stands a fair correlation was found between annual growth rate and rainfall for June, while in others little correlation existed. He found that drought years resulted in a decrease in growth rate the following year, whereas wet years in most cases resulted in an increase in growth rate the same year.

Cary, Wyman, Harper, and Craighead (1932) recognize the effect of prolonged dry periods in the naval stores region on the vigor of longleaf and slash pines and the consequent yield of gum and also the effect of other factors associated with dry periods such as beetle attack and fire which often result in the death of worked trees or in dry-facing (drying out of wood tissue). They state: "Weather Bureau records rate 1931 as the driest year for many years and the first two months in 1932 have been of much the same character. The ground being dried out very deeply and thoroughly. . . . Only small yield of gum is to be expected while the soil is in this condition; faces will dry in unusual numbers; timber may die in some quantity, the latter being helped by insects." Cary (1932a) observed that longleaf pine on deep sands on ridges suffered more from drought than on soils with clay nearer the surface, and more than slash pine. However, an impenetrable hardpan or claypan near the surface stops the downward growth of the tap root of longleaf pine into the permanent water table. The volume of soil above the pan, in which all the tree roots are necessarily located, is relatively small and cannot hold a great amount of water. On such soils the growth of longleaf pine is markedly reduced by prolonged dry periods (Cary, 1932b).

The advisability of light-working of trees, on severe sites during and immediately after droughts was inferred by Cary (1932c, 1933) who also observed heavy mortality and dry-facing in dense stands of slash pine growing on flat ground and old-field following the dry period of 1931 and 1932.

FIELD METHOD AND DESCRIPTION OF STANDS

The growth measurements were obtained from increment borings at breast height (4.5 feet above the ground). Only trees in relatively open stands were measured in order to eliminate, as much as possible, the effects on annual radial growth of initial stand density and the closing of the crowns with increasing age. However, growth curves indicated that even when this precaution was taken a decreasing trend of growth was usually present. Only one boring was taken from each tree. The work of Lodewick (1930) with longleaf pine shows that growth on one radius is about as reliable as data obtained by averaging the growth of four cores taken on different sides of the same trees.

The annual growth rings were measured in the field with a metric scale or with an engineer's scale but when the latter was used the measurements were later converted to the metric system. By measuring the growth in the field as the trees were bored, possible errors due to shrinkage or contortion of the cores as a result of drying were eliminated.

Dominant trees, usually ten, were measured in each stand. The average height of the trees was estimated, and the age obtained from the increment cores. The diameter of each tree was also obtained with a diameter tape.

Measurements were made during the summer of 1934 and they included the 1933 annual ring; but none of the 1934 ring which was in the process of formation. Ring measurements of the trees in the stand near DeRidder, Louisiana, were made on May 8. In Georgia, all measurements were made between May 30 and June 13 with the exception of the stand located 4 miles west of Soperton, which was measured on September 18. The ring measurements in Arkansas were made on May 22 and May 23.

The nature of the stands and their location follows:

LOUISIANA

DeRidder — Loblolly pine
Location of stand: 4.6 miles south of DeRidder.
Location of weather station: Lake Charles, 40 miles south of DeRidder.
Number of trees: 10. Average age in years: 25.
Average diameter in inches: 11.8. Average height in feet: 60.

GEORGIA

Waycross — Slash pine
Location of stand: 11.8 miles north of Waycross.
Location of weather station: Waycross.
Number of trees: 10. Average age in years: 25.
Average diameter in inches: 7.3. Average height in feet: 40.

Waycross — Longleaf pine
Location of stand: 9.2 miles north of Waycross.
Location of weather station: Waycross.
Number of trees: 10. Average age in years: 17.
Average diameter in inches: 8.8. Average height in feet: 30.

Valdosta — Slash pine
Location of stand: 10.5 miles east of Valdosta.
Location of weather station: Quitman, 30 miles west of stand.
Number of trees: 11. Average age in years: 17.
Average diameter in inches: 8.2. Average height in feet: 30.

Cordele — Slash pine
Location of stand: 18 miles south of Cordele.
Location of weather station: Americus, 30 miles northwest of stand.
Number of trees: 10. Average age in years: 20.
Average diameter in inches: 9.0. Average height in feet: 35.

Cordele — Longleaf pine
Location of stand: 18 miles south of Cordele.
Location of weather station: Americus, 30 miles northwest of stand.
Number of trees: 10. Average age in years: 20.
Average diameter in inches: 8.5. Average height in feet: 40.

Soperton — Slash pine
Location of stand: 11 miles northeast of Soperton.
Location of weather station: Dublin, 25 miles northwest of Soperton.
Number of trees: 10. Average age in years: 18.
Average diameter in inches: 8.9. Average height in feet: 35.

Soperton Slash pine
Location of stand: 4 miles west of Soperton.
Location of weather station: Dublin, 20 miles northwest of stand.
Number of trees: 50. Average age in years: 9.
Average diameter in inches: 8.1. Average height in feet: 29.

ARKANSAS

Calico Rock Shortleaf pine
Location of stand: 2 miles southwest of Calico Rock.
Location of weather station: Calico Rock.
Number of trees: 10. Average age in years: 32.
Average diameter in inches: 8.2. Average height in feet: 45.

Madison County Shortleaf pine
Location of stand: 5 miles west of Eureka Springs.
Location of weather station: Eureka Springs, 10 miles north of stand.
Number of trees: 10. Average age in years: 35.
Average diameter in inches: 7.7. Average height in feet: 45.

Carroll County Shortleaf pine
Location of stand: 9 miles west of Eureka Springs.
Location of weather station: Eureka Springs, 7 miles west of stand.
Number of trees: 8. Average age in years: 25.
Average diameter in inches: 8.3. Average height in feet: 45.

CLIMATE OF LOCALITIES STUDIED

Climatological data were obtained from weather stations, nearest to the stands studied, whose records were complete for the period of time included in the study. The locations of the weather stations with respect to the stands are given above.

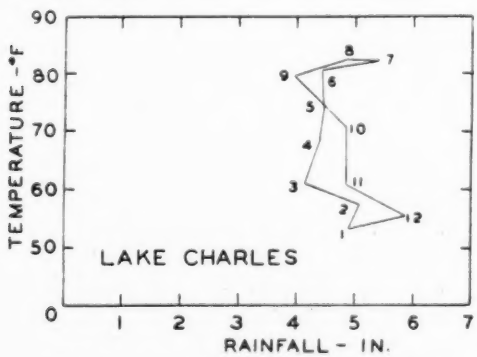

FIG. 1. A climograph for Lake Charles, Louisiana. The average monthly temperature is plotted over the average rainfall for each month. The twelve points are connected by straight lines in chronological order. The figure is based on monthly averages for the 16 years from 1918 to 1933 for which growth data are available. Variation in rainfall due to differences in the number of days in each month was adjusted by correcting the monthly averages to a 30-day month. The numbers on the climograph indicate the month, 1 for January, 2 for February, etc.

SOUTHERN LOUISIANA

The character of the climate of southwestern Louisiana can best be understood by examining the climograph for Lake Charles (Fig. 1). The average annual rainfall at Lake Charles is 57 inches and the average annual temperature is 68° F. The climograph is a convenient form to show graphically the climate of a place. It is constructed by plotting the average temperature of each month over the average rainfall and connecting the points by lines in their chronological order. The points representing each month are num-

bered beginning with January as 1, February as 2, and so on. The climograph shows the monthly distribution of rainfall and monthly temperature for the 16 years from 1918 to 1933. The average monthly rainfall is between 4 and 6 inches; and the average monthly temperature ranges from 53° F. in January (number 1) to 84° F. in August (number 8), a total mean range of 30°. The lowest rainfall occurs in March (number 3) and September (number 9), and the heaviest rainfall comes in December (number 12) and July (number 7).

SOUTHERN GEORGIA

The average annual rainfall for Waycross is 48 inches; and the average annual temperature is 68° F., the same as Lake Charles, Louisiana. Figure 2 shows average monthly distribution of rainfall and the average monthly temperatures. The range of monthly rainfall is from 2 to over 7 inches, and the range of average monthly temperature is from 53 to 82° F. October (number 10) and November (number 11) are the driest months, with about 2 inches of rainfall, while July (number 7) has over 7 inches. July and August (number 8) are the two warmest months with average temperatures of 81 and 82° F., respectively. The average rainfall for the spring months, March, April, and May (number 3, 4, and 5) is relatively low and fluctuations of rainfall for these months are often reflected in the growth of pine.

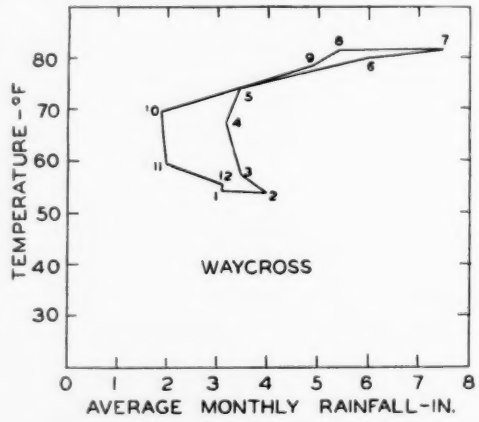

FIG. 2. A climograph for Waycross, Georgia. Average monthly temperature is plotted over the average monthly rainfall. The figure is based on averages for the 17 years from 1917 to 1933 corrected to 30-day months. Waycross is located in the extreme southern part of the state. The range of average monthly temperatures is approximately the same as for southern Louisiana, but the rainfall distribution is characterized by a definite dry period in October and November, and a rainy season through June, July, and August. The heavy summer rain is partly monsoonal from the Gulf, and partly convectional.

There is a relatively large increase in temperature from March to April (numbers 3 to 4). These two points should be kept in mind in interpreting the reason for the high association between annual radial growth and the two climatic factors for the early spring period.

NORTHERN ARKANSAS

The average annual rainfall for Calico Rock is 41 inches; and the average annual temperature is 59° F. which is 9° lower than for southern Louisiana and southern Georgia. As can be seen in Figure 3 the range of average monthly rainfall is from about 2.5 inches in February (number 2) to 5 inches in April (number 4), while temperature ranges from 38° F. in January (number 1)

to 81° F. in August (number 8). Rainfall is relatively low in the winter and early spring and high in April and May (numbers 4 and 5).

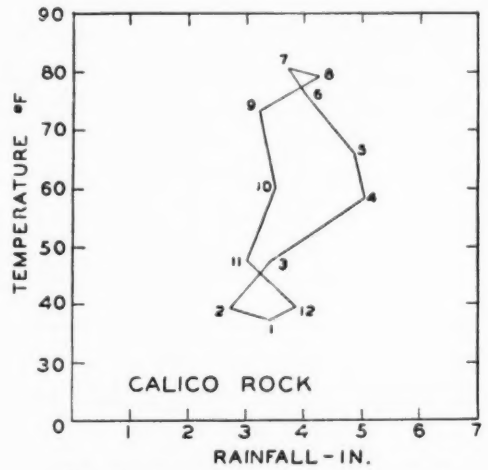

FIG. 3. A climograph for Calico Rock, Arkansas. Average monthly temperature is plotted over the average monthly rainfall. The figure is based on averages for the 17 years from 1917 to 1933 corrected to 30-day months.

Calico Rock is on the Ozark Plateau in the northern and central part of the state. The range of average monthly temperatures is greater than at Lake Charles, Louisiana, being between 40 and 45° F. The heaviest rainfall occurs in April and May (numbers 4 and 5), while the lowest occurs in February (number 2). Total rainfall for Calico Rock is approximately 44 inches a year.

ANALYTICAL METHODS

Growth data for DeRidder, Louisiana, and climatic data for Lake Charles were correlated by graphic methods in which the average annual growth of 10 trees was plotted over the year in which the growth took place—1918 to 1933—and the points connected by straight lines. The rainfall for two periods, January to June and July to December, inclusive, were then plotted over time above the growth curve. No consistent relationship appeared to exist between growth and rainfall for either of the two periods. Average periodic temperature and growth compared in a similar manner failed to show definite and consistent relationship. It was then decided to use moving totals of rainfall by 3, 4, and 5-month periods; and moving averages of temperature for the same periods. These climatic data were plotted over time and the fluctuations of the curves connecting the points were compared with the annual fluctuations of the growth curve. Definite positive relationship was seen to exist between rainfall for certain of the early spring periods and growth. However, it was impossible by the graphic method alone to determine whether the rainfall of January to May, inclusive, or February to June, inclusive, was most clearly associated with growth. Many graphs of this type were made for the loblolly pine data from near DeRidder, Louisiana, and the slash pine data obtained near Waycross, Georgia, before it was finally decided that a mathematical method of measuring degree of association between the climatic factors and growth was necessary.

Other investigators, Douglass, Huntington, and Diller, have used the correlation coefficient[3] to measure the relationship between each of the climatic factors and growth in a time series.

[3] Correlation coefficient: $r = \frac{S(xy)}{Sx^2 \cdot Sy^2}$, Fisher (1934) where S = sum, x = deviation of either rainfall or temperature, and y = the percentage deviation of annual growth.

The chief objection to the use of the correlation coefficient in the measurement of degree of association in a time series, is that we must assume that the relationship between the two variables (rainfall or temperature and growth) is linear. This objection, often raised by statisticians, is well founded. A linear relationship is one that can best be expressed by a straight line. For radial growth and rainfall correlation, equal increases or decreases in rainfall are associated with proportional deviations in growth. Almost everyone will agree that in general the relationship of growth to rainfall is curvilinear; increases in rainfall up to a certain amount will result in proportionate increases in growth, but above that amount continued increases in rainfall will not result in increases in growth to the same degree; finally, a point in the increase of rainfall may conceivably be reached where there is actually a diminution of growth.

The point under discussion is illustrated in Figure 4. Given the hypothetical curve of annual growth over rainfall A B C D in which the relationship between the two variables, considered as a whole is curvilinear; any group of growth and rainfall data that could be represented by the segment A B has a linear relationship which could be measured by the correlation coefficient. Such a correlation would be positive. If the data were represented by the segment B C the correlation coefficient would indicate no association, when actually a relationship does exist but it is curvilinear. By the same method, data represented by the segment C D would give a negative correlation coefficient.

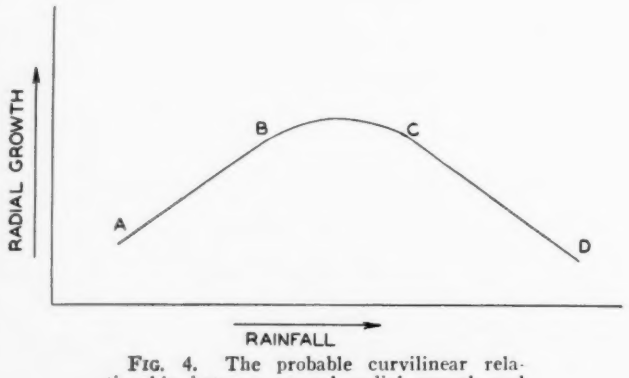

FIG. 4. The probable curvilinear relationship between annual radial growth and rainfall.

In this study it has been assumed that, with the species concerned, and the climate, soils, and topographic positions of the areas, rainfall has never been excessive for the periods involved, and that the relationship between radial growth and either of the two climatic factors can best be represented by a straight or nearly straight line. With this assumption the correlation coefficient has been used to measure association between growth and the climatic factors.

The standard error of the correlation coefficient was not used because of the short time series involved; that is, the small number of samples employed when temperature, or rainfall, and growth are considered one variate. The time series vary from 7 to 17 years, which means a sample of 7 to 17 variates. The statistical significance of the correlation coefficient for small samples can

best be determined by the use of Fisher's table of the values of the correlation coefficient for different levels of significance. Correlation coefficients falling in the 0.02 level of significance, or less, were considered statistically significant in all of the following analyses; this level of significance means that the probability of the correlation arising, by random sampling, from an uncorrelated population is only 2 out of 100.

ANALYSIS OF DATA

SOUTHERN LOUISIANA

When the average annual radial growth of the 10 loblolly pine trees near DeRidder, Louisiana, was plotted over time, and a straight line fitted to the points, it was evident that the growth rate was decreasing (Fig. 5). Total rainfall for all groups of months showed no such decreasing trend. In fact the smoothed curve of rainfall for January to April, inclusive, was horizontal (this curve is not shown in Fig. 5, but rather the actual rainfall is represented by broken lines). Since rainfall over the 16-year period was not decreasing, it was evident that the decreasing trend of growth rate was due to some other factor, or factors, than cyclic change of climate; the most likely factor being the closing of the stand as it grew older (it was 25 years old in 1933). By using the deviations of the average annual growth from the curve of growth the effects of the decreasing trend were eliminated. The use of the actual deviations of average annual growth from the 16-year arithmetic average would have eliminated almost entirely the effects of annual fluctuations of periodic rainfall and temperature. The average annual growth for the 10 trees from 1918 to 1933 was 6.4 mm. Had the deviations of the average growth for each year been calculated from this figure, there would have been a preponderance of positive deviations in the first part of the time series and a preponderance of negative deviations in the last part. The correlation coefficient calculated from these deviations would have shown little or no association between growth and the climatic factors, when actual association exists. Since the effects of the downward trend of growth were eliminated by the use of the annual percentage deviations from the best straight line that could be fitted to the data, this analysis is concerned with the effects of annual fluctuations of periodic rainfall and temperature on annual growth, and not with the effects of cyclic change, which might be reflected in secular trend of growth.

The correlation coefficients for growth and rainfall, and for growth and temperature were determined by using monthly rainfall and average temperature for March, April, May, and June, and the annual percentage deviation of growth from the growth curve (Table 1). The highest correlation between radial growth and monthly rainfall was found for May, the correlation coefficient being +0.557, which is statistically significant, according to Fisher's

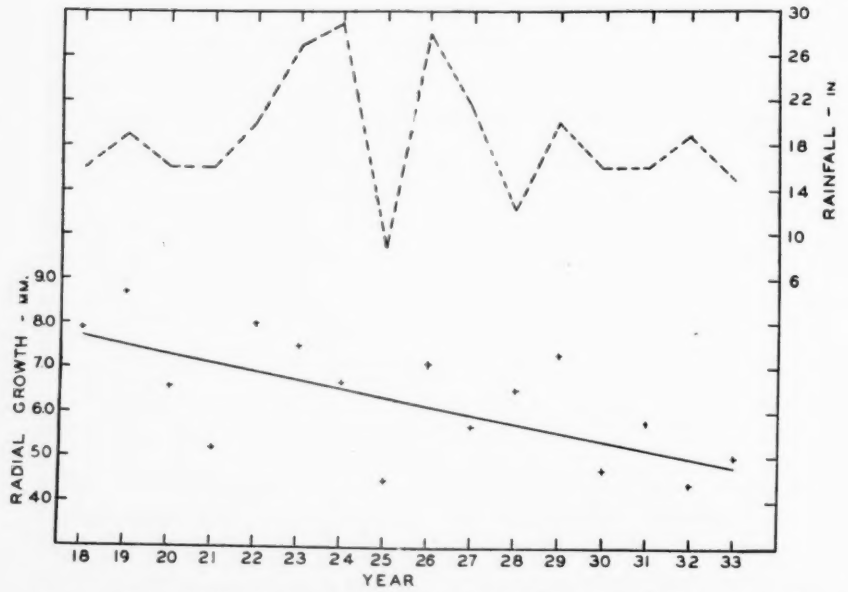

FIG. 5. The relation between radial growth of loblolly pine at DeRidder, Louisiana, and rainfall at Lake Charles, Louisiana. The solid line shows the trend of radial growth of 10 trees from 1918 to 1933. The broken line shows the fluctuations of the total rainfall during January to April, inclusive, for the same years. The growth curve was fitted by the method of least squares and shows a downward trend, while a smoothed curve of rainfall (not shown) maintains an even trend.

table of levels of significance. Correlation coefficients for the other months were not statistically significant. Average monthly temperature showed little correlation with growth. When the deviations of the rainfall by 4-month periods were correlated with growth, rainfall for February to May was found to give the highest correlation coefficient, +0.479, but it is not statistically significant. The highest negative correlation of temperature and growth was for the same 4-month period (Table 2).

The curve of correlation coefficients for 4-month periods indicates by its slope that the rainfall in May has more influence on growth than rainfall during the previous December (Fig. 6); on the basis of this observation the correlation coefficients for 5-month periods of rainfall and growth were calculated; in which, the rainfall for January to May, inclusive, of the current year was found to have a relatively high positive correlation with growth,

TABLE 1. The relation of annual radial growth to rainfall and temperature of single months as measured by the correlation coefficient, DeRidder, Louisiana.[4]

Growth with:	Month			
	March	April	May	June
Rainfall	.....	+0.275	(+0.557)[5]	—0.027
Temperature	(—0.216)	—0.100	+0.003	+0.153

[4] Based on the growth of 10 trees from 1918 to 1933.

TABLE 2. The relation of annual radial growth to rainfall and temperature for four-month periods as measured by the correlation coefficient, DeRidder, Louisiana.[5]

Growth with:	Oct., Nov., Dec., Jan.	Nov., Dec., Jan., Feb.	Dec., Jan., Feb., Mar.	Jan., Feb., Mar., Apr.	Feb., Mar., Apr., May	Mar., Apr., May, June	Apr., May, June, July	May, June, July, Aug.
Rainfall.....	+0.122	+0.101	+0.420	+0.454	(+0.479)[5]	+0.367	+0.342	+0.196
Temperature...	.....	.....	.....	—0.463	(—0.470)	—0.210	.....	.....

[5] In Tables 1 to 7, inclusive, values in parentheses are the highest, and values in italics are statistically significant. According to Fisher's tables of values of correlation coefficients for different levels of significance, the probability of this correlation arising, by random sampling, in an uncorrelated population is 2 in 100 or less.

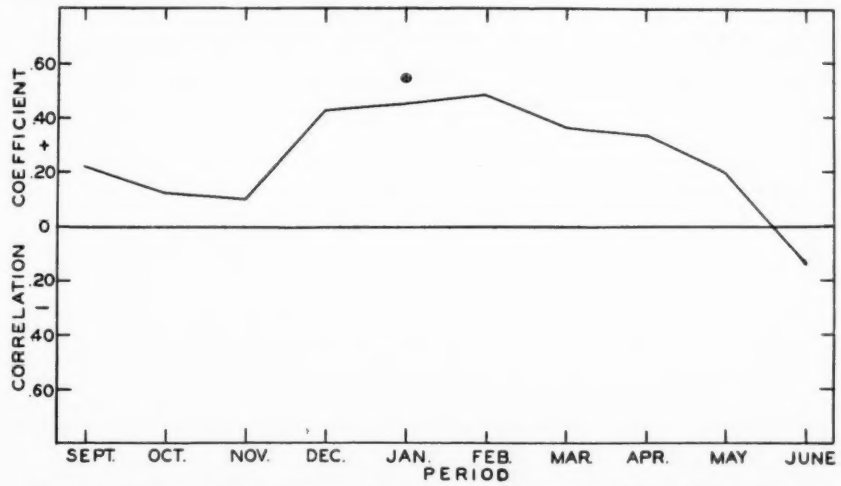

FIG. 6. The association between the annual radial growth of 10 loblolly pine trees near DeRidder, Louisiana, and rainfall for 4-month periods at Lake Charles, Louisiana, as measured by the correlation coefficient. The period is indicated by the abbrevation of the first month, i.e., Sept. = September, October, November, and December of the year previous to which the growth was made, while Jan. = January, February, March, and April of the year in which the growth was made. The inscribed cross indicates the correlation coefficient for growth and rainfall during January to May, inclusive.

$r = +0.545$ (Table 3). This value is just under the minimum for statistical significance. The correlation coefficient for January to May is given in Figure 6 as an inscribed cross showing its relation to the values for the shorter climatic periods.

TABLE 3. Correlation coefficients indicating the relation of annual radial growth to rainfall and temperature for five-month periods, DeRidder, Louisiana.[6]

Growth with:	Previous Year		Current Year			
	January to May	February to June	December to April	January to May	February to June	March to July
Rainfall.....	(—0.559)	+0.394	+0.394	+0.545	+0.431	.....
Temperature....	.....	.....	—0.388	—0.421	(—0.445)	—0.240

[6] Based on the growth of 10 trees from 1918 to 1933.

The relation of total rainfall and average temperature of January to May, inclusive, to growth is shown on logarithmic scale in Figure 7. In this graph the radial growth is corrected for a decreasing trend, while temperature and rainfall do not exhibit a decreasing trend. Positive fluctuations of rainfall are seen to be associated with positive fluctuations of growth while positive fluctuations of temperature are associated with average or less than average growth. The low rainfall in 1921 and 1925, particularly the latter, was reflected markedly in the growth rate. The temperatures for these two years were above average. High temperature in 1927 was associated with a decreased growth rate although rainfall was slightly above the average. The low rainfall of 1928 was in part offset by the low temperature, and growth increased over the previous year. The lack of positive correlation between rainfall and growth in 1931 and 1933 can probably be attributed to inverse variation in temperature. Low temperature and low rainfall in 1931 were associated with an increase in growth over the previous year, while an increase in temperature and a slight increase in rainfall in 1932 was associated with a decrease in growth. Of particular interest in Figure 7 is the low range of temperature, only about 7° F. However, only slight rises in temperature in April and May are associated with low growth in 1921 and 1927.

Smoothed curves of growth and rainfall show positive agreement in their fluctuations. The curves were left unsmoothed in Figure 7 in order to bring out the magnitude of the annual fluctuations.

The relation of the percentage deviation of the annual growth to the de-

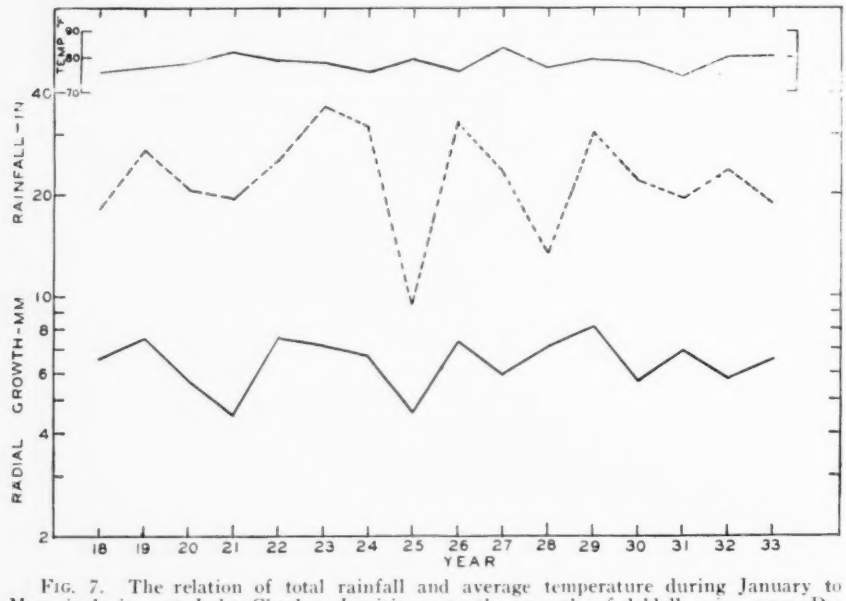

FIG. 7. The relation of total rainfall and average temperature during January to May, inclusive, at Lake Charles, Louisiana, to the growth of loblolly pine near DeRidder, Louisiana. The lower solid line represents growth corrected for decreasing trend due to the closing of the stand. The broken line represents total rainfall during January to May, inclusive. The upper solid line shows the trend of average temperature for the same period. Growth, rainfall, and temperature are plotted on logarithmic scale.

viation of the rainfall is shown in Figure 8, left side. The trend line indicates the strength of the association. During the 8 years in which the rainfall for January to May, inclusive, was above average, growth was above average 7 years; while of the 7 years when rainfall was below average, growth was below average 4 years. On the right, in Figure 8, a similar graph of percentage deviation of growth and the deviation of the average temperature is shown. In the 8 years in which temperature was below average, growth was above average 7 years; while in the 8 years that temperature was above average, growth was below average 5 years. Considering the two graphs together, low rainfall and high temperature account for nine of the combinations when growth was less than average.

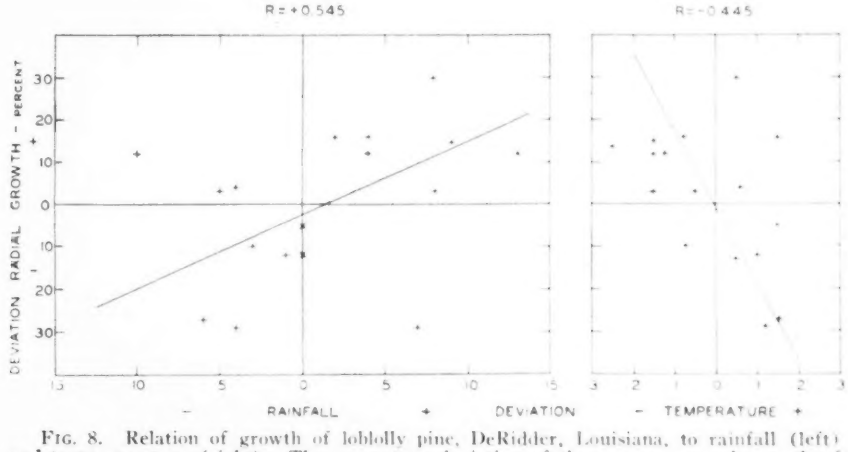

FIG. 8. Relation of growth of loblolly pine, DeRidder, Louisiana, to rainfall (left) and to temperature (right). The percentage deviation of the average annual growth of 10 trees from their trend line is plotted over the deviation from the average of the annual precipitation of January to May, inclusive. The graph on the right is based on the same growth data plotted over the deviation of the average temperature from the average periodic temperature of the entire time series, 1918 to 1933. Both lines were fitted on the basis of the dependent variable, growth.

The three variables, growth in percentage of the average based on the curve, total rainfall for January to May, inclusive, and average temperature for the same period, are brought together in Figure 9. Growth in percentage of the average for each year was plotted on the total rainfall and average temperature, and smooth lines (isopleths) fitted to the points at 5 per cent intervals (points are not shown). In general, if the lines in such a chart are parallel to the temperature axis that variable has little influence on growth, which in such a case would vary with rainfall. The opposite extreme would be for the isopleths to be distributed parallel to the rainfall axis in which case growth would vary with temperature. Although Figure 9 is based on only 16 points (16 years), an intermediate condition to the two outlined above obtains. The heavy line, 100 per cent isopleth, indicates conditions of average growth. This isopleth shows that growth remains average if temperature increases rapidly with increases of rainfall, while if rainfall remains constant and temperature increases, annual growth will decrease. Annual growth re-

mained average when rainfall and temperature increased from 12 inches and 64° F., respectively, to 22 inches and 69° F, respectively. The highest annual growth occurred when periodic rainfall was between 20 and 30 inches with the temperature between 64 and 67° F. However, the supporting data are insufficient for this to be considered the climatic optimum.

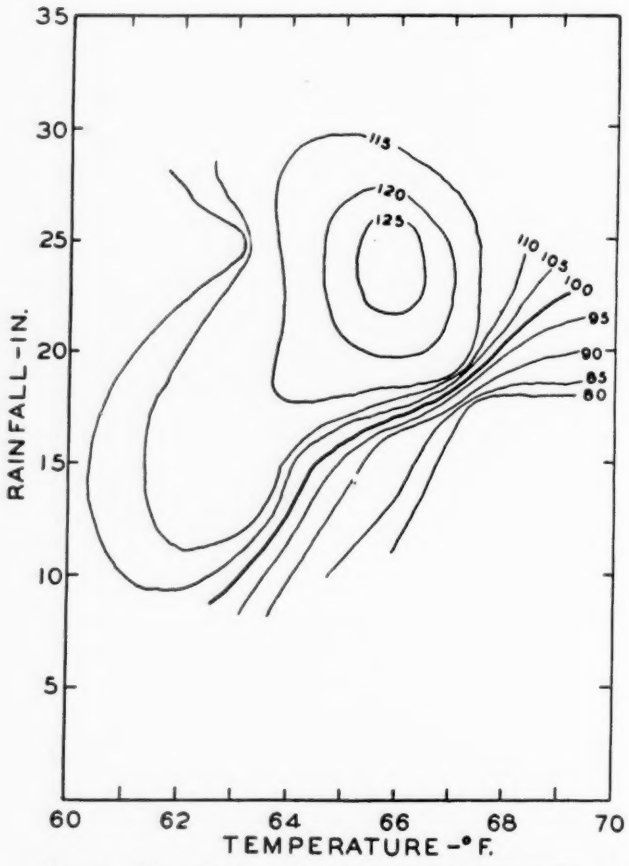

FIG. 9. The relation of both rainfall and temperature to growth of loblolly pine, DeRidder, Louisiana. The annual growth expressed as a percentage of the average is plotted on the total rainfall and average temperature for February to May, inclusive, of each year. Isoplethic lines (as contour lines) were fitted to the percentage values at 5 per cent intervals. The heavy line (100) indicates climatic conditions associated with average radial growth rates.

The isoplethic lines indicate that both rainfall and temperature for February to May, inclusive, have an influence on growth rate for the current year. Average growth rate is maintained if increases in temperature are accompanied by increases in rainfall.

SOUTHERN GEORGIA

The growth of 10 slash pine trees near Waycross, Georgia, during 1918 to 1933 showed a trend of increasing growth. There was no reason to believe that the same rainfall period as in southwestern Louisiana (January to May, inclusive) would have the highest correlation with the growth of slash pine in southern Georgia. It was necessary to follow a similar procedure in eliminating months and groups of months to find the one in which the climatic factors were most closely associated with radial growth. This was accomplished, as before, by using climatic data for single months and groups of months (averages in the case of temperature) in correlation with growth. The correlation coefficients for single months and groups of months are shown in Table 4. The correlation coefficient for annual growth and the rainfall of February to April, inclusive, is higher, +0.750, than for single months or longer periods. This value is statistically significant.

TABLE 4. Correlation coefficients showing the relation of annual radial growth of slash pine to monthly and periodic rainfall near Waycross, Georgia, based on the growth of 10 trees from 1918 to 1933.

January	February	March	April
+0.113	*(+0.670)*[7]	+0.517	+0.243
December, January, February	January, February, March	February, March, April	March, April, May
+0.432	*+0.710*	*(+0.750)*	+0.443

December, January, February, March	January, February, March, April	February, March, April, May
+0.570	*(+0.730)*	*+0.625*
December, January, February, March, April	January, February, March, April, May	February, March, April, May, June
+0.466	*(+0.668)*	+0.507

[7] See footnote 5.

The apparent sensitivity of the annual radial growth of slash pine near Waycross, Georgia, to the spring rainfall of the year in which the growth took place suggested the possibility of determining the effect of the previous year's rainfall and temperature on current annual growth. This was done by calculating correlation coefficients for rainfall and growth, and temperature and growth by 3-month moving climatic periods beginning with January to March, inclusive, of the year previous to that in which the growth was made. Ten periods of the previous year and 11 periods of the current year were used. The results are shown in Table 5, and the correlation coefficients are plotted in Figure 10. The effect of early spring rainfall on growth is evidenced by the high positive correlation for January to March, inclusive, and February to April, inclusive, of the current year. The effect of rainfall during the years previous to those in which the growth occurred is brought out by the relatively high positive correlation between growth and the rainfall of the previous summer. This may be due to the effect of favorable, or unfavorable, rainfall during the summer and late summer on the elaboration and storage of foods that are used in the rapid building of new woody tissue the following spring.

A relatively high negative correlation exists between the average temperature of July to September of the previous year and growth, while the average temperature of June to August of the current year has a still higher negative correlation with growth, the correlation coefficient being —0.800, which is statistically significant. The correlation analysis clearly indicates that rain-

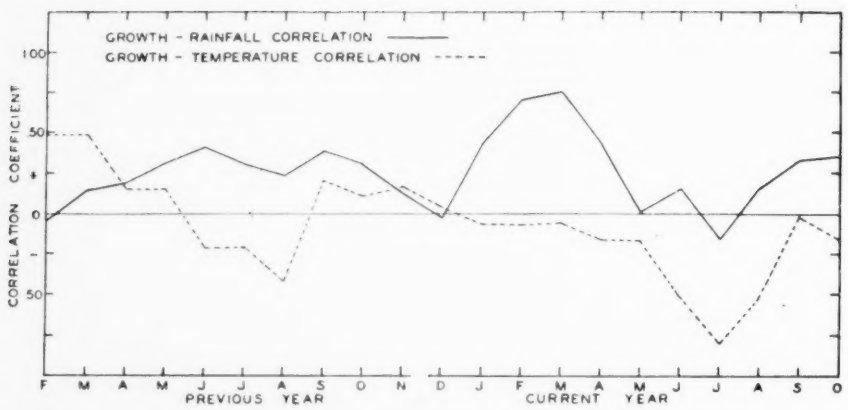

FIG. 10. The association between annual radial growth of slash pine and rainfall and temperature for 3-month periods at Waycross, Georgia, as measured by the correlation coefficient. The period is indicated by the first letter of the second month (F = period of January, February, and March). The 10 periods on the left half of the figure are for the year previous to the one in which the growth took place, and end with the period of October to December of the previous year. The current year correlation begins with the period of November and December of the previous year plus January of the current year.

fall in the early spring and temperature in the summer are closely associated with radial growth.

A graphic representation of the strength of association between radial growth and the rainfall of February to April is given in Figure 11. The percentage deviation of the annual growth is plotted over the annual deviation of

TABLE 5. The relation between the annual radial growth of slash pine for 16 years and the two climatic factors, Waycross, Georgia.

Period	Correlation coefficients for radical growth and	
	Rainfall	Temperature
January, February, March	—0.027	0.485
February, March, April	0.136	0.492
March, April, May	0.193	0.151
April, May, June	0.306	0.155
May, June, July	(0.414)	0.218
June, July, August	0.302	—0.218
July, August, September	0.235	(—0.415)
August, September, October	0.398	0.216
September, October, November	0.317	0.115
October, November, December	0.137	0.162
November, December, January	—0.078	0.027
December, January, February	0.432	—0.064
January, February, March	*0.710*	—0.053
February, March, April	(*0.750*[8]	—0.043
March, April, May	0.443	—0.154
April, May, June	0.045	—0.168
May, June, July	0.156	—0.506
June, July, August	0.154	(*—0.800*)
July, August, September	0.155	—0.524
August, September, October	0.338	—0.020
September, October, November	0.357	—0.165

[8] See footnote 5.

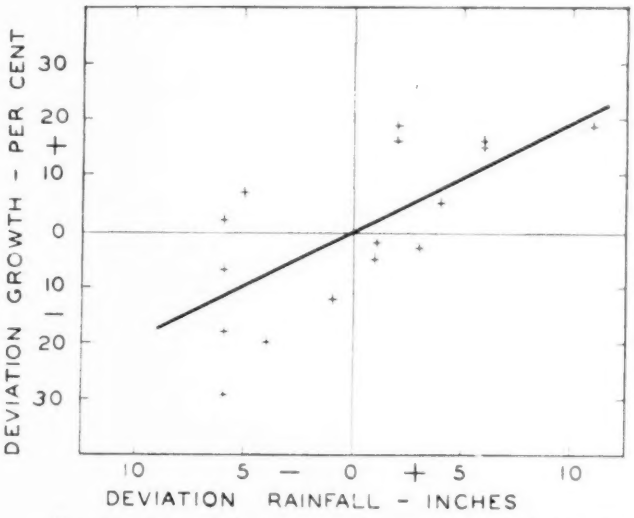

FIG. 11. The relation between the percentage deviation of annual growth of slash pine from the trend line and the deviation of annual rainfall from the average of February to April, Waycross, Georgia. The line representing the trend was fitted to the points on the basis of the dependent variable, growth; based on the average annual growth of 10 trees for 16 years.

periodic rainfall from the mean. A horizontal curve would indicate no relationship between growth and rainfall. A decrease in the rainfall during February to April, inclusive, of 5 inches below the average results in a deviation of growth from the average of 10 per cent, while an increase in periodic rainfall of 5 inches above average is associated with an increase in growth of 10 per cent.

The correlation coefficients indicate that rainfall during February to April, inclusive, is most influential in determining the amount of growth. The rainfall for this period is plotted over years in Figure 12 with the annual growth corrected for an increasing trend.

The annual growth of slash pine near Waycross, Georgia, shows the closest agreement with rainfall (February to April, inclusive) of any of the

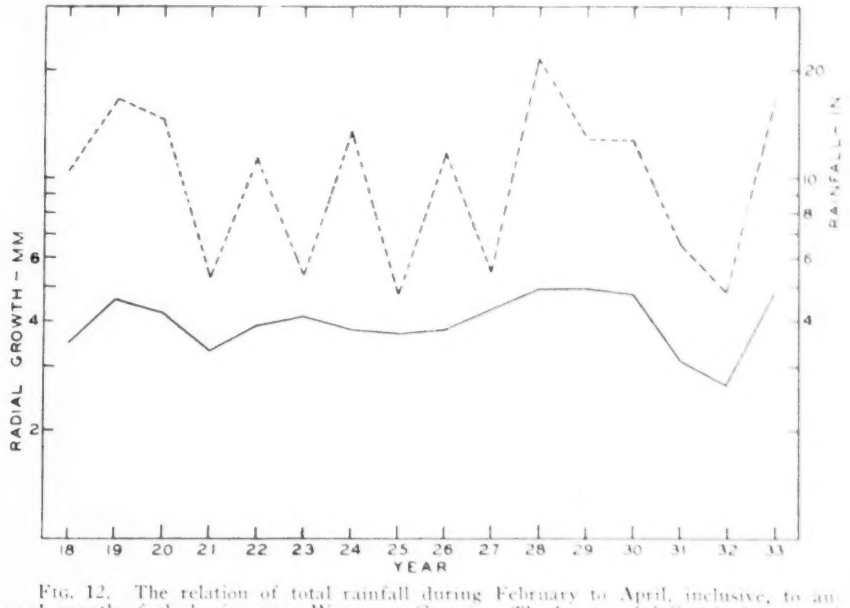

FIG. 12. The relation of total rainfall during February to April, inclusive, to annual growth of slash pine near Waycross, Georgia. The lower solid line is for annual growth corrected for a slight increasing trend. The broken line is for periodic rainfall. Both growth and rainfall are plotted on logarithmic scale.

stands studied. If the annual fluctuations of rainfall for the years 1921 to 1927, inclusive, are disregarded, almost complete agreement with growth obtains. High rainfall and growth in 1919, 1920, 1928, 1929, 1930, and 1933; and low rainfall and growth in 1921, 1931, and 1932 are conspicuous (Fig. 12). Smoothed curves of the two variables follow similar trends almost completely.

An isoplethic chart of growth on rainfall and temperature for February to April indicates that growth varies with rainfall, and that temperature at that time has little influence (Fig. 13). This is to be expected since the correlation coefficient for growth and temperature in only —0.043, which for practical purposes indicates no correlation. Rainfall of 12 inches or more is reflected in average or above average growth.

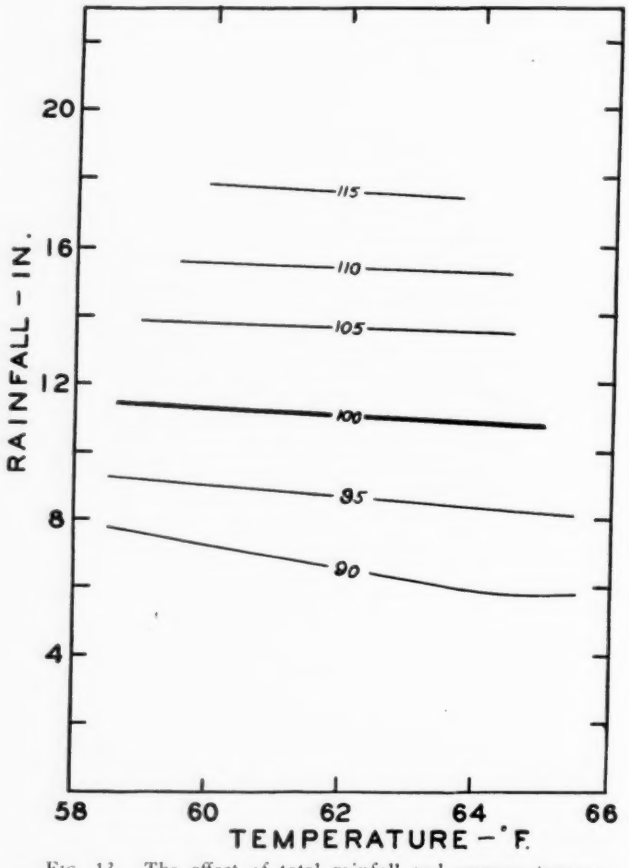

FIG. 13. The effect of total rainfall and average temperature during February to April, inclusive, on the annual growth rate of slash pine near Waycross, Georgia, as illustrated by an isoplethic chart. The chart was made by plotting the annual growth as a percentage of the average on the points representing the total rainfall and average temperature of February to April of each year. Smooth lines (isopleths) at 5 per cent intervals were fitted to the points. The isopleths indicate that radial growth is directly associated with rainfall for the period; and that it is affected but little, if at all, by the range of temperatures that obtained for the period from 1917 to 1933.

The extremely low growth of longleaf pine in 1931 and 1932 near Waycross, Georgia, coincides with a similar feature in the growth of slash pine in the same locality. The annual growth of slash pine near Valdosta, Georgia, and rainfall for February to April, inclusive, are shown in Figure 14. Rough agreement obtains between rainfall and growth. Notable features are the low rainfall and growth in 1925, 1931, and 1932; and the high rainfall and growth in 1919, 1920, 1923, 1928, 1930, and 1933. The correlation coefficient for annual growth and rainfall during February to April, inclusive, is +0.540, which is higher than that for the overlapping periods on either side (Table 6).

TABLE 6. The relation between annual radial growth and the rainfall of 3-month periods in Georgia as measured by the correlation coefficient.

Location	Species	Time Series Years	Growth—Rainfall Correlation			
			January February March	February March April	March April May	April May June
Valdosta..	Slash pine.....	16	0.273	(0.540)	0.433	0.052
Waycross..	Longleaf pine..	13	0.404	(0.514)	0.138	—0.115
Waycross..	Slash pine.....	16	*0.710*	(*0.750*)[9]	0.443	.....
Soperton ..	Slash pine.....	7	0.618	0.566	0.486	(0.649)
Cordele...	Longleaf pine..	12	—0.161	0.213	(0.259)	0.159
Cordele...	Slash pine.....	12	0.251	0.515	(0.523)	0.416

[9] See footnote 5.

This value is not statistically significant as measured by the criterion previously used, but it is close, being only 0.030 below the minimum correlation coefficient that is considered significant.

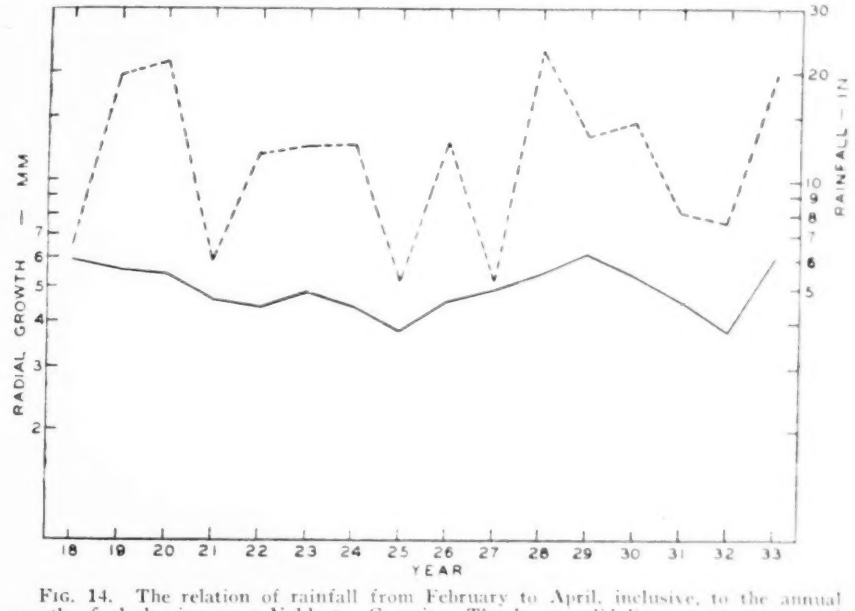

FIG. 14. The relation of rainfall from February to April, inclusive, to the annual growth of slash pine near Valdosta, Georgia. The lower solid line represents annual growth corrected for a slight increasing trend. The broken line represents periodic rainfall. Both growth and rainfall are plotted on logarithmic scale.

The highest correlation coefficient was obtained for the annual growth of 50 slash pine trees near Soperton, and the rainfall of April to June, inclusive. The correlation coefficient for that period was +0.649. The value for January to March, inclusive, +0.618, was also high. Both values fall below the minimum for statistical significance previously used because of the few years involved. Temperature during April to June, inclusive, had the highest negative association with the growth of these trees, the correlation coefficient being —0.413.

Rainfall during February to April or March to May appears to have about equal influence on the growth of slash pine near Cordele, Georgia; the correlation coefficients being +0.515 and +0.523, respectively. A slight positive correlation between growth and temperature during January to February and April to June is apparent. The coefficients being +0.360 and +0.354, respectively (Table 7).

TABLE 7. The relation between annual radial growth and the average temperature of 3-month periods in Georgia as measured by the correlation coefficient.

Location	Species	Time Series Years	Growth—Temperature Correlation			
			January February March	February March April	March April May	April May June
Valdosta..	Slash pine.....	16	0.303	(—0.209)	0.033	0.082
Waycross..	Longleaf pine..	13	0.154	0.120	0.355	(—0.141)
Waycross..	Slash pine.....	16	—0.053	—0.043	0.184	(—0.145)
Soperton..	Slash pine.....	7	0.203	—0.223	0	(—0.413)
Cordele...	Longleaf pine..	12	0.225	—0.161	(—0.331)	0.121
Cordele...	Slash pine.....	12	(0.360)	0.246	0.038	0.354

The combined effects of both rainfall and temperature on the growth of slash pine and longleaf pine in Georgia is shown in Figure 15. This is a composite isoplethic chart of climatic data for the period of February to April from four weather stations, and the percentage deviation of the average annual radial growth from the growth curves of both species. The chart is based on growth of 110 trees in 7 different stands and on time series of from 7 to 18 years.

The isopleths indicate that temperature has little influence on growth, with the possible exception of a slightly beneficial effect of high temperature during the early spring. Growth is influenced markedly by rainfall, average growth being associated with approximately 12 inches of precipitation. Rainfall of between 12 and 20 inches results in greater than average growth, while more than 20 inches of rain apparently causes a decrease in growth rate on the whole. However, the writer is inclined to minimize the apparent decrease in growth when the rainfall is greater than 20 inches on the basis that a heavy rainfall in the spring is often followed by a dry summer with high temperatures, which tend to counterbalance the beneficial effects of the heavy spring rainfall. Periods of heavy spring rainfall are often preceded by a relatively dry late winter which tends to lessen the effects of an abundant rainfall in the spring. These conditions were generally apparent to the writer while tabulating and analyzing the climatic data. Likewise, a very dry and hot late summer will probably cause less foods to be stored and in that way influence the growth the next spring irrespective of the current climatic conditions.

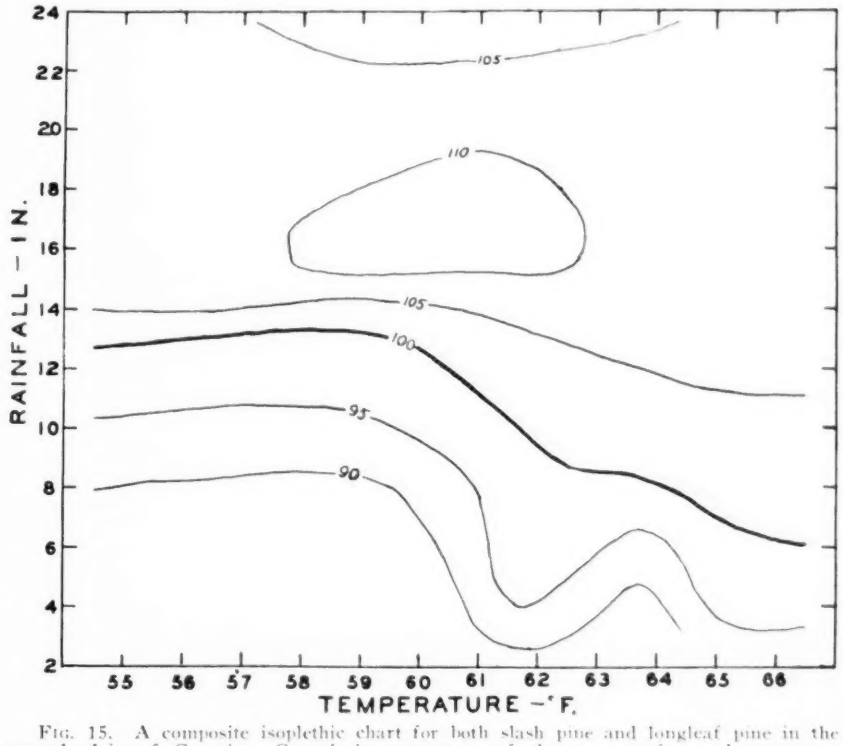

FIG. 15. A composite isoplethic chart for both slash pine and longleaf pine in the coastal plain of Georgia. Growth in percentage of the average for each year was plotted on the points representing the total rainfall and average temperature for February to April, inclusive, of each year. Smooth lines (isopleths) at 5 per cent intervals were then fitted to the points. The isopleths indicate climatic conditions associated with similar growth rates. The chart is based on 110 trees of 2 species; periods of from 7 to 16 years; and climatic data from 4 stations. The isopleth of 110 per cent growth indicates most favorable conditions of rainfall and temperature.

NORTHERN ARKANSAS

The rainfall for April to June, inclusive, has the highest positive correlation with annual growth of shortleaf pine near Calico Rock, Arkansas. The correlation coefficient was +0.328, which is not statistically significant. Temperature shows little correlation with growth (Fig. 16).

An 18-year time series was possible with the data from Madison County, Arkansas. The highest positive correlation between growth and rainfall was again found for the period of April to June, inclusive, for which the correlation coefficient is +0.574, which is statistically significant. The greatest negative correlation between growth and temperature was found for May to July, inclusive, for which the correlation coefficient is —0.422 (Fig. 17). The effect of above-average temperatures in the late summer was to decrease growth also. Low rainfall was reflected in decreased growth in 1920, 1922, 1926, 1930, and 1931, while high rainfall was associated with greater than average growth in 1927, 1928, and 1929.

The correlation coefficients for the growth of shortleaf pine near Eureka Springs in Carroll County, Arkansas, and rainfall indicate that rainfall from

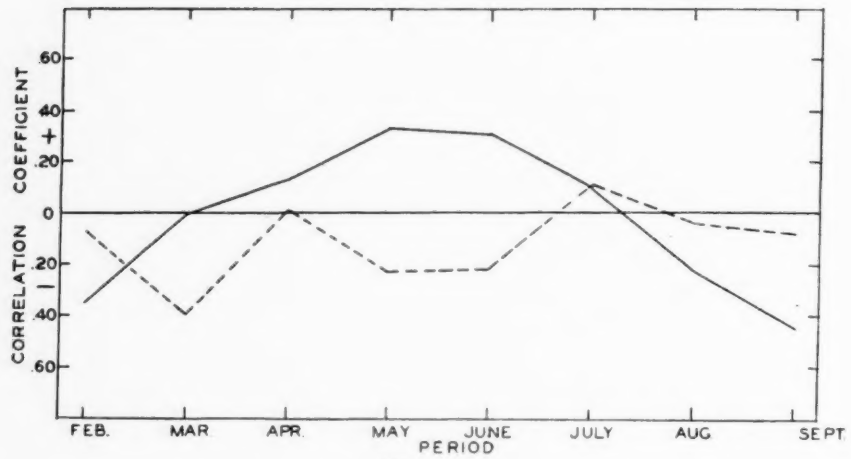

FIGURE 16

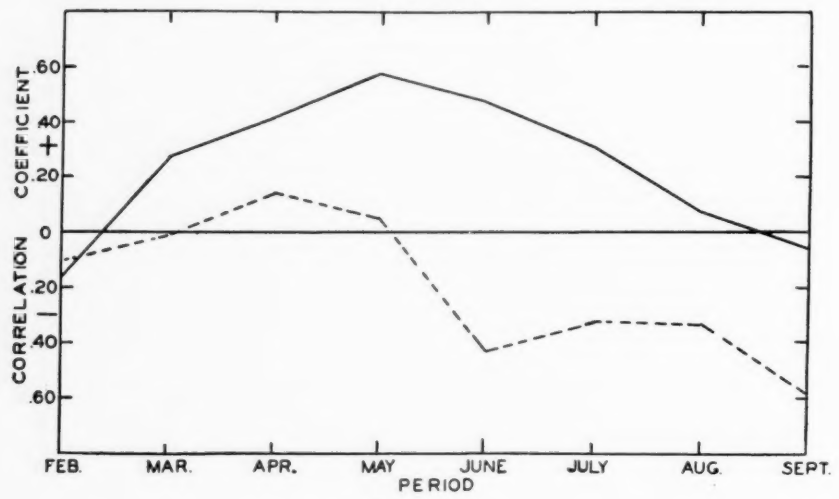

FIGURE 17

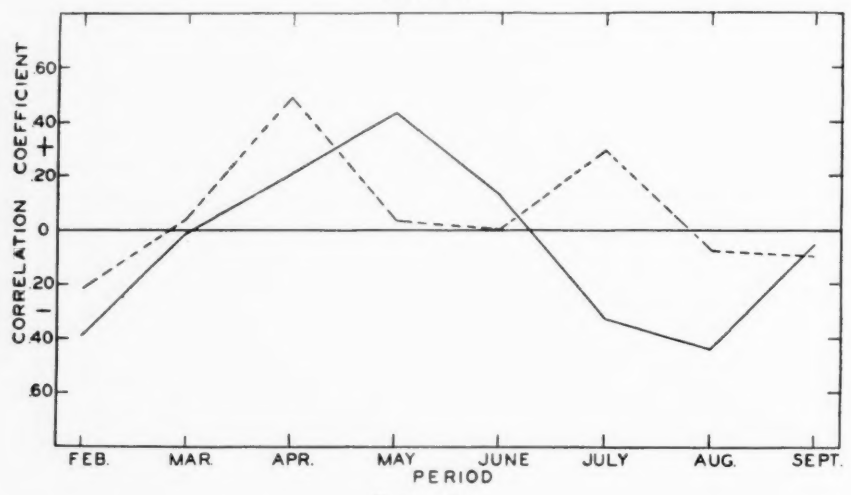

FIGURE 18

FIGS. 16, 17, and 18. The association between annual radial growth of shortleaf pine and rainfall and temperature for 3-month periods at Calico Rock (Fig. 16), and in Madison (Fig. 17), and Carroll (Fig. 18) counties, Arkansas, as measured by the correlation coefficient. Rainfall and temperature data from Eureka Springs were correlated with growth in Madison and Carroll counties. The period is indicated by the middle month, i.e., Feb. = January, February, and March of the year when the growth took place. The solid line is for growth-rainfall correlation and the broken line is for growth-temperature correlation.

April to June is again most closely associated with growth; the correlation coefficient is +0.434 (Fig. 18). However, temperature for the periods of March to May and June to August have a positive association with growth. The correlation coefficients are +0.487, and +0.293, respectively. None of the above correlation coefficients are statistically significant. On the basis of present information the writer does not attempt to explain the positive temperature correlation, except to point out that low temperatures during the growing season may be of such magnitude as to cause a decrease in growth especially in stands on certain topographic positions, relatively moist sites or northern slopes.

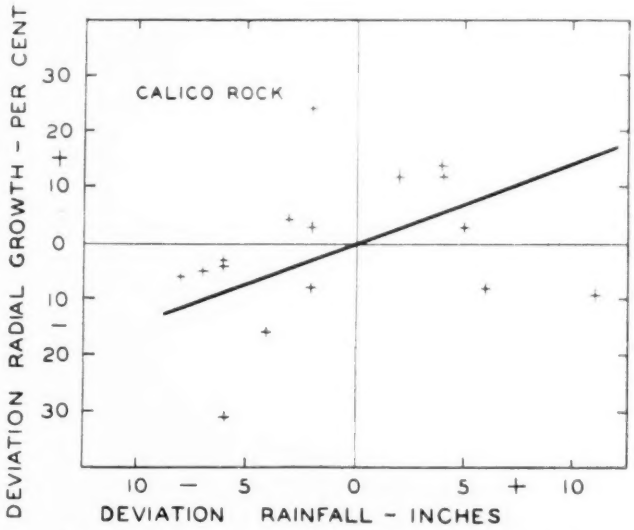

FIG. 19. Relation between the percentage deviation of the annual growth from the trend line of 10 trees near Calico Rock, and the annual deviation of rainfall from the average during April to June, inclusive. The line showing the association was fitted to the points on the basis of the dependent variable, growth. The correlation coefficient for growth and rainfall is + 0.574, and is statistically significant.

The relation of percentage deviation of annual growth to the deviation of rainfall for April to June, inclusive, is given in Figures 19, 20, and 21. Figure 19 is for the stand near Calico Rock, Figure 20 is for the stand in Madison County, and Figure 21 is for the stand in Carroll County. The correlation coefficients for growth and rainfall of these distributions are +0.544, +0.328, and +0.487, respectively.

Of the 10 years when rainfall was below average at Calico Rock, growth was less than average 7 years, and of the 7 years when rainfall was above average, growth was above average 5 years (Fig. 19).

The data for the stand in Madison County do not indicate as good agreement between rainfall and growth as do the data for the stand near Calico Rock (Fig. 20). During the 11 years when rainfall was below average, growth was below average 6 years, and of the 5 years when rainfall was above average, growth was above average 4 years. Of the 11 years when the periodic rainfall was below the average, the growth of trees in the stand in Carroll County was below average 6 years, and of the 4 years when rainfall was above average, growth was above average 3 years (Fig. 21).

The relation between both rainfall and temperature, and annual growth is shown in the composite isoplethic chart for the 3 stands (Fig. 22). This

chart is based on the average growth rates of 28 trees in 3 stands and climatic data from 2 weather stations for 17 years. The climatic period is April to June, inclusive. Positive association between early spring temperature and annual growth in the stand in Carroll County (Fig. 18) and in the stand in Madison County (Fig. 17) is reflected in the downsweep of the isopleths when the total rainfall was under 16 inches, and the average temperature increased from 66 to 70° F. Average and above average growth is associated with rainfall of 14 inches and more.

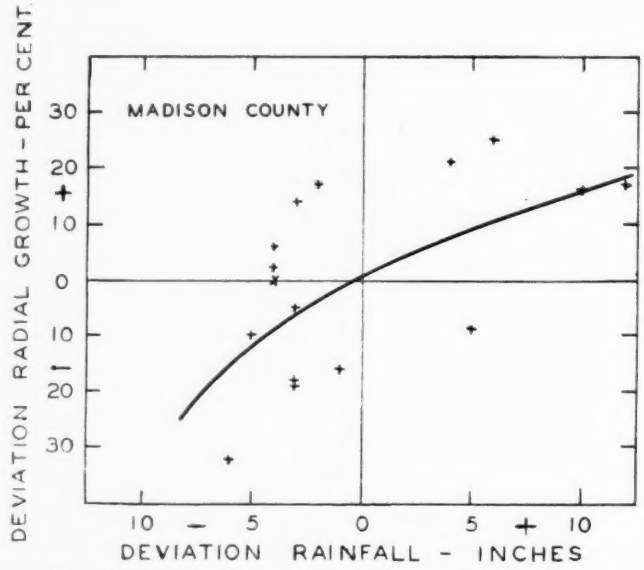

FIG. 20. Relation between the percentage deviation of the annual growth of 10 trees in Madison County from the trend line and the annual deviation of rainfall from the average in April, May, and June at Eureka Springs. The correlation coefficient for growth and rainfall is + 0.328, which is not statistically significant.

SUMMARY AND CONCLUSIONS

An analysis of the relation between the annual radial growth of the 4 southern pines and periodic rainfall and temperature was made for 148 trees in 9 localities and 11 stands in Louisiana, Georgia, and Arkansas.

Correlation analysis, employing the correlation coefficient as a measure of association between two variables, was used to determine the period of the year in which climatic factors were most influential in determining the annual radial growth. Graphic methods were then employed to illustrate the relationships.

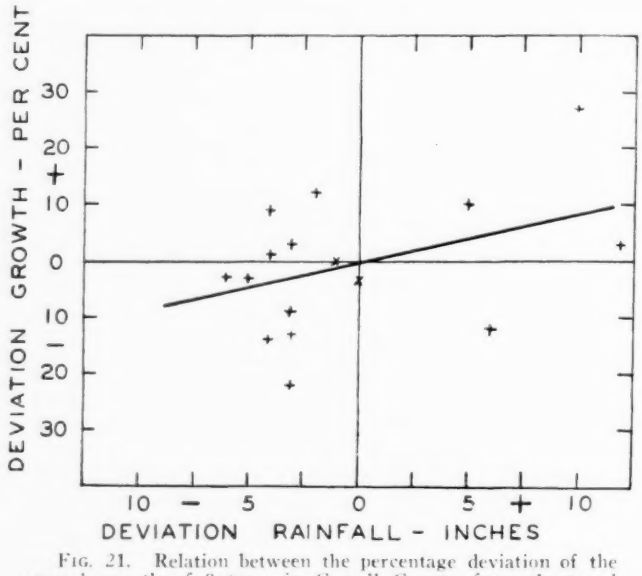

FIG. 21. Relation between the percentage deviation of the annual growth of 8 trees in Carroll County from the trend line and the annual deviation of rainfall from the average during April to June, inclusive, at Eureka Springs. The correlation coefficient for growth and rainfall is + 0.487, and is not statistically significant.

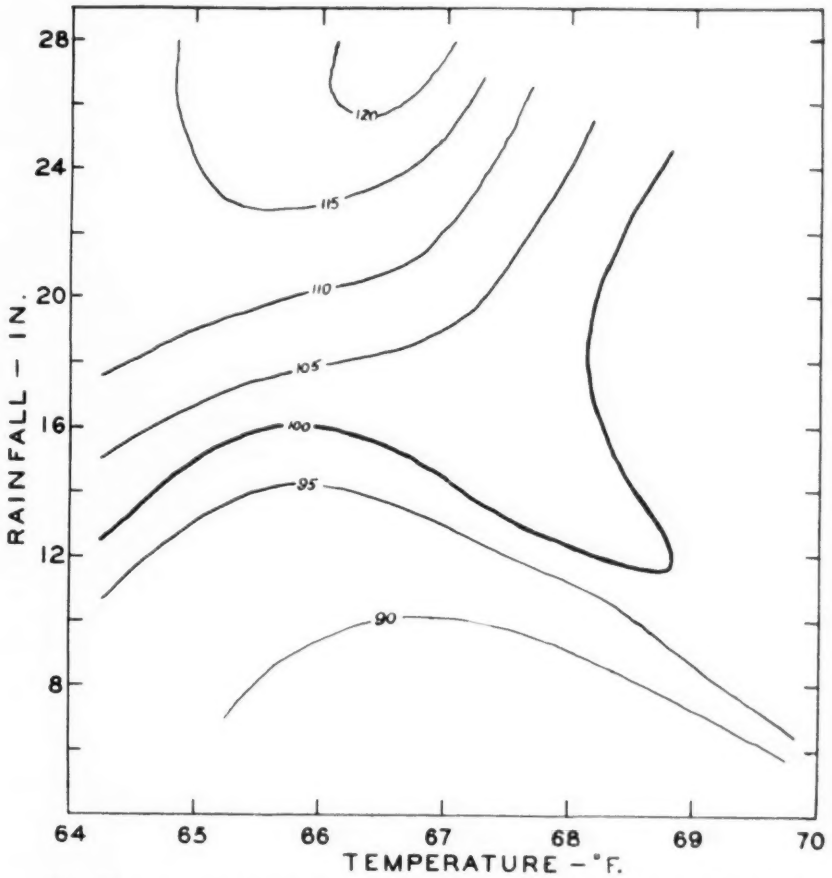

FIG. 22. Composite isoplethic chart for three stands of shortleaf pine in Arkansas. Growth as a percentage of the average for each year, based on the annual radial growth of 28 trees from 1917 to 1933, is plotted on total rainfall and average temperature for April to June, inclusive. The isopleths indicate that rainfall of approximately 14 inches, or above, is associated with average or above average annual growth.

The annual growth of loblolly pine in southwestern Louisiana is influenced most by fluctuations of the total rainfall during January to May, inclusive, the association is positive, that is, increases in rainfall above the mean usually result in an increase in growth under any given conditions of temperature. Less than average rainfall usually results in sub-normal annual growth under any given condition of temperature. Deviations of average temperatures for the same period are negatively correlated with growth. High temperatures are usually associated with low growth and low temperatures are associated with more than average growth.

The annual growth of slash pine and longleaf pine in the Coastal Plain of Georgia is influenced most by rainfall in the early spring—February to April, inclusive. The relationship is positive. The average temperature of the summer period—June to August, inclusive—has the highest negative correlation with growth. High temperatures are associated with low growth.

The temperature of the previous summer is negatively correlated with annual growth, but less strongly than current summer temperatures in the stands studied.

In northern Arkansas, the rainfall for April to June, inclusive, gave the highest positive correlation with the annual growth of shortleaf pine, while the relation of periodic temperature to annual growth exhibits much variation.

Good association was found between annual radial growth and the climatic factors when the trend of radial growth was linear.

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